LABORATORY STUDIES ON THE FEEDING BEHAVIOUR OF JUVENILE CAPE HORSE MACKEREL *Trachurus trachurus capensis*

by

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This dissertation is submitted for the degree of

MASTERS OF SCIENCE

In the Department of Zoology
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Declaration

This dissertation is my own work and the results discussed were carried out at Marine and Coastal Management (MCM), Department of Environmental Affairs and Tourism between 1999–2001. The experiments described were conducted by myself with assistance from technical staff at MCM acknowledged on pp v - vi. All counts, identification and processing of the data were also conducted by myself. The database used to manipulate the data collected was developed by my supervisor Dr C. D. van der Lingen. I was responsible for the data analysis, and I lay claim to concepts, hypotheses and conclusions, in consultation with my supervisors, in this dissertation.

Signed by candidate

TEMBELA MAPUKATA (MISS)

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ABSTRACT

Laboratory studies were conducted on juvenile horse mackerel to examine feeding selectivity and rates of zooplankton consumption of two size classes of fish. Fish were fed a variety of natural zooplankton assemblages and sequential subsampling of water in the experimental tanks provided estimates of prey concentration. Video observations were used to examine feeding behaviour and to investigate the feeding response of horse mackerel to various food types and prey sizes.

Juvenile horse mackerel are particulate feeders, and both small and large juveniles exhibited size selectivity with large prey removed faster than the small prey although very large prey (> 7.0 mm total length (*TL*)) were not selected by small juveniles. Clearance rate of large juveniles were higher than those of small juveniles for all prey sizes. The clearance rate of large juveniles 175 mm *TL* showed a sigmoidal relationship with prey size, being 3.18 l fish.$^{-1}$ min^{-1} for prey 0.50-1.70 mm *TL*, increasing rapidly over a prey size range of 1.70-1.80 mm *TL* and levelling off at 10.23 l fish.$^{-1}$ min^{-1} for prey > 1.80mm *TL*. The clearance rate of small juveniles 90 mm *TL* exhibited a dome-shaped relationship with prey size, and ranged from 1.63 l fish.$^{-1}$ min^{-1} for prey < 0.88 mm, to 3.55 l fish.$^{-1}$ min^{-1} for prey size > 0.88 mm and lowers to 2.0 l fish.$^{-1}$ min^{-1} with prey >4.0 mm. The low clearance rates of large prey (> 7.0 mm *TL*) by small juveniles are attributed to prey handling difficulties. Clearance rate was inversely proportional to prey concentration for both small and large juveniles, and may be a result of learnt behaviour, where the horse mackerel first familiarized themselves with available prey in the tank and then concentrated on specific prey sizes or types, or the decrease in prey concentration made it possible for them to efficiently remove their prey. Swimming speeds of large juveniles were proportional to both prey concentration and prey size, whereas small juveniles swam at the same speed irrespective of prey concentration or size.

Estimating the nutritional value of ingested prey depends on the accuracy of the relationships relating prey size to carbon content. The clearance rate values were used in conjuction with biomass estimates of zooplankton in southern Benguela to estimate consumption rates and hence the time required to attain daily ration for horse mackerel juveniles. In this study, the time required to attain daily rations ranging between 2 and 6 % wet body mass per day (*WBM* d^{-1}) was estimated, and for 4% *WBM* d^{-1} it ranged between 0.54-1.0 hours for small juveniles and 1.83-2.27 hours for large juveniles

The feeding behaviour of juvenile horse mackerel was compared to that of anchovy *Engraulis capensis* and sardine *Sardinops sagax*, other major planktivores in the southern Benguela ecosystem. Horse mackerel are obligate particulate feeders, whilst anchovy and sardine are capable of both particulate and filter feeding. All three species feed selectively on larger prey when particulate feeding. A comparison of weight standardized clearance rate versus prey size for all three species indicates that juvenile horse mackerel are less efficient than anchovy and sardine at removing zooplankton prey. This study enables a better understanding of the feeding behaviour

of small horse mackerel, their position in the zooplankton feeding guild and their role in ecological pathways of the southern Benguela ecosystem.

CHAPTER 1

INTRODUCTION

1.1: Introduction

Horse mackerel are among the most abundant and widespread fish species worldwide, occurring in all oceans with the exception of the cold waters of the Arctic and Antarctic. As with several clupeoid species (e.g. anchovy and sardine), horse mackerel are particularly abundant in the major upwelling regions (e.g. California, Humboldt, Canary and Benguela) (Fig. 1.1) (Crawford 1989).

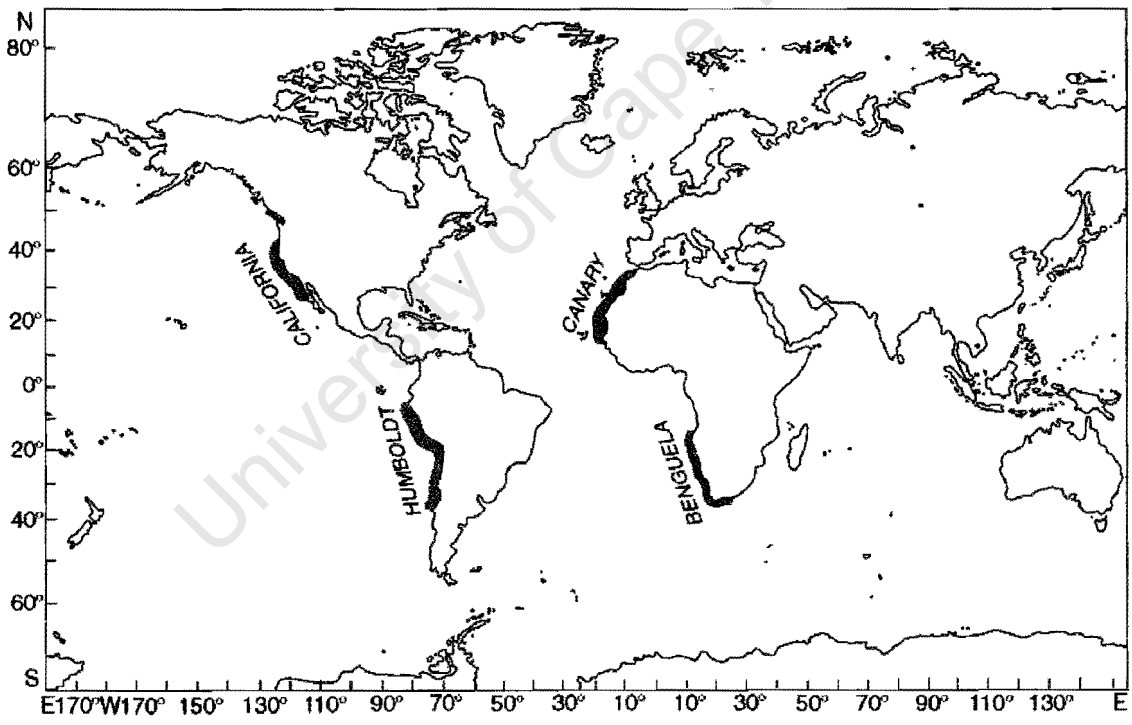

Fig. 1.1. Map illustrating major upwelling regions of the world (From Jarre - Teichmann *et al* 1998).

Horse mackerel belong to the Carangid family, which includes several popular angling species such as kingfish *Caranx* spp. and yellowtail *Seriola* spp. (Crawford 1989, Kerstan and Leslie 1994). They are fast-swimming, schooling fish that can attain lengths of up to 70 cm, and are characterized by a curved lateral line with enlarged scute-like scales (Crawford 1989).

Two species occur in southern African waters, Cape horse mackerel *Trachurus trachurus capensis* and Cunene horse mackerel *Trachurus trecae*. Both have contributed to the large south-east Atlantic fisheries for several decades, from 1956 onwards (Crawford 1989). Although the distributions of the two species overlap (Crawford *et al.* 1987, Kerstan and Leslie 1994), *T. trecae* occurs primarily in the vicinity of the Cunene River and northwards into Angolan waters, whereas *T. t. capensis* is confined to the Benguela system and the Agulhas Bank (Crawford 1989, Kerstan and Leslie 1994). The present study is focused on the Cape horse mackerel, known locally as maasbanker. They are an important component of the ecosystem, representing a major food source for predatory fish such as Cape hake *Merluccius* sp. (Konchina 1986, Payne *et al.* 1987, Roel and McPherson 1988, Pillar and Wilkinson 1995), as well as seals and whales (David 1987, Sekiguchi *et al.* 1992).

1.2: Stock distribution and identity of horse mackerel in the southern Benguela ecosystem.

Cape horse mackerel are widely distributed in southern African waters, extending from the southern Angolan and Namibian shelf waters southwards to the Agulhas Bank and eastwards to the vicinity of East London (Konchina 1986, Hecht 1990, Naish 1990, Naish *et al.* 1991, Kerstan and Leslie 1994, Barange *et al.* 1998). They have distinct size-related differences in their depth distribution, small fish preferring shallow waters (Badenhorst and Smale 1991). From the information obtained during pelagic surveys conducted by Marine and Coastal Management (MCM) on the South and West coasts Barange *et al.* (1998), showed marked differences in the distribution of horse mackerel by size (Fig 1.2). Recruits (<10 cm total length, *TL*) are generally limited to the area between the Orange River and Mossel Bay, whereas the majority of adults (>30 cm) reside east of Mossel Bay, principally along the shelf edge. Juvenile fish (10 - 20 cm) are concentrated inshore along the coasts of the Western and Southern Cape whereas fish of 20 - 30 cm occur over the whole South Coast shelf. The surveys reported by Barange *et al.* (1998) were, however, restricted to the inner shelf on the West coast and did not extend beyond the shelf edge.

Although the entire habitat range of horse mackerel was not covered, Barange *et al.* (1998) were able to suggest a conceptual model of its life history, with recruits concentrated more on the on the West Coast, juveniles over the central Agulhas Bank and the adults farther east.

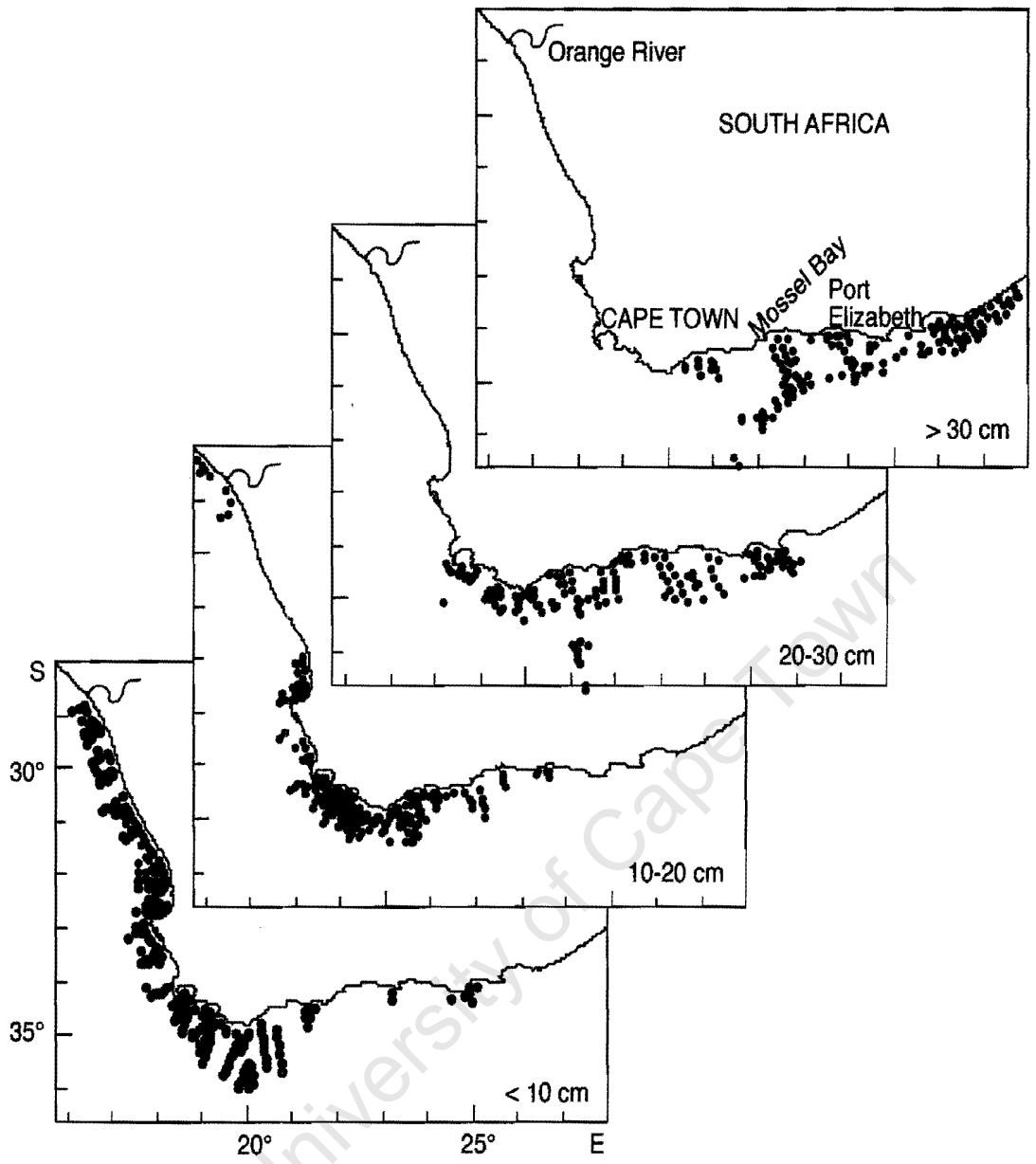

Fig. 1.2. Map showing the distribution of Cape horse mackerel by size derived from acoustic/midwater trawl surveys in South African waters, 1984-1996 (From Barange *et al.* 1998).

The stock structure of Cape horse mackerel off South Africa remains a controversial topic. Differential catch distributions led to the assumption that there were two separate stocks, one off the west coast of southern Africa and the other over the Agulhas Bank (Centurier – Harris and Crawford 1974, Draganik 1977, Crawford 1980, 1981). An

investigation of maturation patterns and otolith sizes supported this hypothesis (Naish 1990), but mitochondrial DNA analysis indicated that there was only one stock, south of the Orange River (Naish 1990), supporting the viewpoints of Kinloch *et al.* (1986), Payne (1986) and Crawford (1989). Morphometric analyses gave inconclusive results (Naish 1990). Therefore, further research is required to resolve this, perhaps using random amplified polymorphic DNA analyses (Kerstan and Leslie 1994).

1.3: The horse mackerel fishery

The horse mackerel fishery in South Africa started in 1929, and it developed in the mid–1940s in response to the wartime demand for canned food (Crawford 1989). The South African south coast demersal trawl industry began targeting horse mackerel in the 1960s, as did foreign trawlers, but it was only from mid- 1966 onwards that records were kept by one of the fishing companies in the area (Hecht 1976). Total research catches of Cape horse mackerel from the three different fisheries in South African waters, pelagic catches starting from 1950, bottom water trawl as from 1958 on wards and midwater trawl from the 1990 (Fig. 1.3).

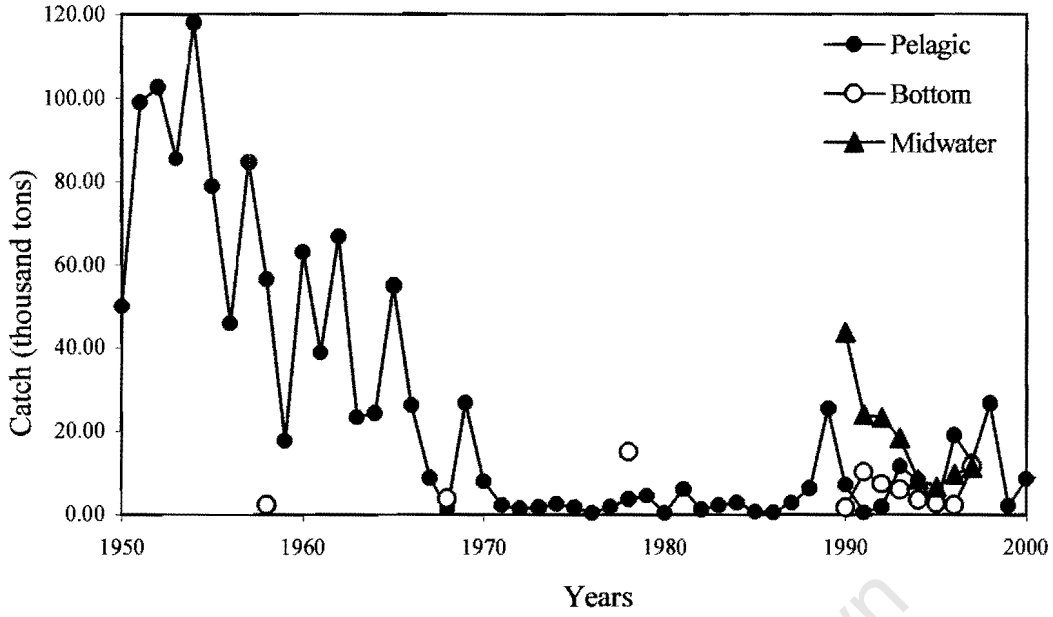

Fig. 1.3. Catches of Cape horse mackerel fisheries (pelagic, midwater and bottom), (Data from C. van der Lingen and S. du Plessis, MCM, pers. comm.).

From the 1970s, horse mackerel have become a bycatch of both the pelagic and demersal fisheries. Purse-seine gear is used off the West Coast to catch the pelagic juveniles that shoal near the surface whereas adults are caught over the Agulhas Bank with midwater and bottom trawl nets (Crawford 1989). Horse mackerel congregate close to the seabed during the day where they are caught by bottom trawl nets (Konchina 1986, Crawford 1989), they rise off the bottom into the water column at night, where they are more readily available to midwater trawling. In Namibia, horse mackerel are caught by midwater trawl and represent their largest fishery (Boyer and Hampton 2001).

The development of local and export markets led to increased interest in this resource. Consequently MCM undertook modelling studies of the dynamics of the horse mackerel

population in order to provide sound scientific and management advice (Barange *et al.* 1998). Initially, the assessment of horse mackerel was hampered by lack of reliable long-term datasets. Although catch per unit effort (*cpue*) and catch data were available from four fleets (South African inshore and offshore demersal, the midwater trawl and a Japanese fleet), the data were regarded as unusable for stock assessment because they were not accurate and in most cases horse mackerel were an undirected by-catch of trawl fisheries directed at hake or other stocks (Kerstan and Leslie 1994).

From 1991 to 1994, four acoustic assessment cruises were carried out, as well as commercial and bottom trawl surveys (Barange *et al.* 1998). For stock assessment purposes, acoustic sampling was subject to bias due to diel changes in vertical distribution of horse mackerel. This behaviour resulted in low and imprecise abundance estimates. Neither bottom trawl nor acoustic indices could be treated as reliable independent estimates of abundance, but a combination of both indices may be the only effective means of assessing the abundance of horse mackerel (Barange *et al.* 1998).

1.4: Biology

1.4.1: Life cycle and spawning

Horse mackerel can live for longer than 10 years and grow up to 70cm long and in excess of 3 kg in weight (Crawford 1989). Length–at–50% maturity (LM_{50}) varies between 32 and 43cm (Hatanaka *et al.* 1983, Uozumi *et al.* 1984, 1985, Payne 1986, Hecht 1990, Naish 1990). The species appears to have two major spawning peaks in South African

waters and timing appears to differ between the eastern and western Agulhas Bank (Fig. 1.4) (Barange *et al.* 1998). The main spawning peak is in August to February on the Western Agulhas Bank and in June to November on the Eastern Agulhas Bank (Hecht 1990). Horse mackerel larval abundance along the Western and Southern Cape between June and October (Shelton 1986) indicate that spawning is closer inshore in winter than in summer (Barange *et al.* 1998). Baird (1978) suggested an onshore migration of horse mackerel in winter, possibly related to their spawning behaviour, as is the case for mackerel *Scomber japonicus* (Geldenhuys 1973).

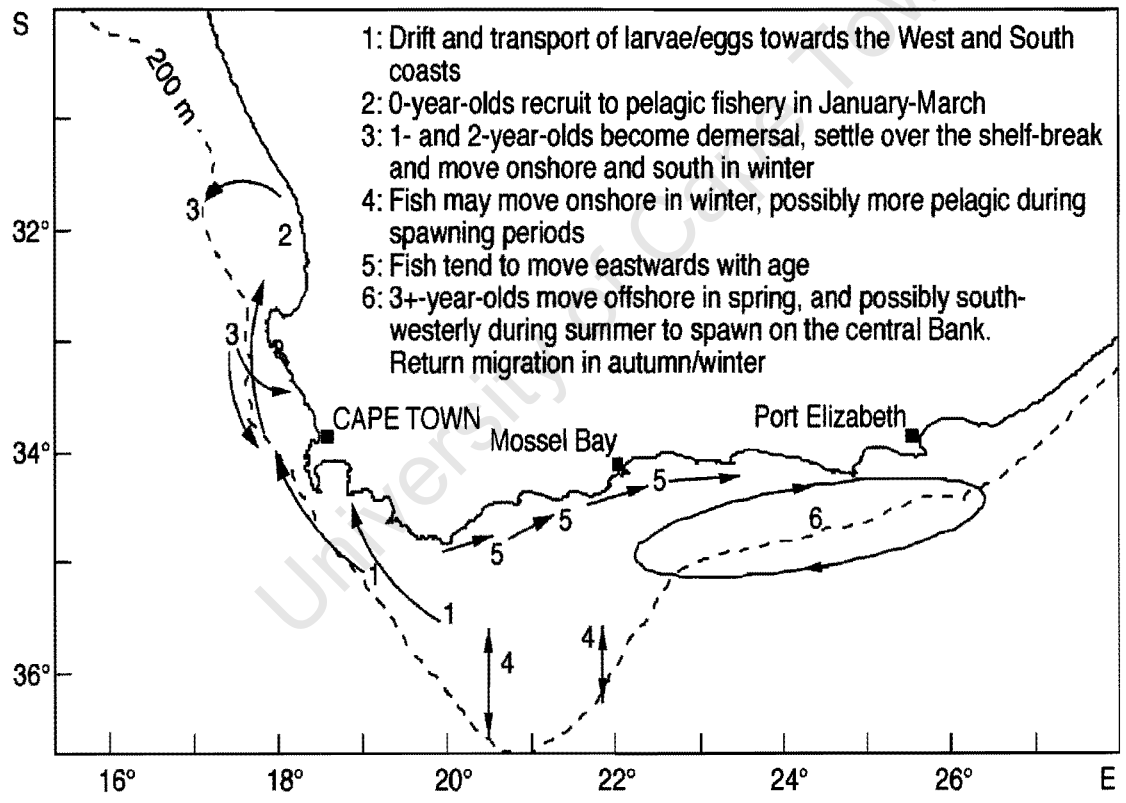

Fig. 1.4. Map showing a conceptual model postulating migration and spawning strategies of Cape horse mackerel (From Barange *et al.* 1998).

During summer, eggs and larvae of horse mackerel over the western and central Agulhas Bank appear to be transported northwards in the shelf-edge jet current along West Coast similar to the reproductive products of sardine and anchovy (Fowler and Boyd 1998). Their utilization of the West Coast as a nursery area is shown by peaks in catches of juvenile horse mackerel in purse-seine landings from January to March. It is postulated that horse mackerel move offshore as they mature, before recruiting to the demersal fishery on the West Coast at 1-2 years of age. Thereafter, there is a southward shift in their distribution from summer to winter suggesting that a portion of that population migrates south in winter (Barange *et al.* 1998). Juveniles recruit to the inshore demersal fishing grounds on the South Coast and they move offshore and eastwards as they grow. After maturation they enter the spawning cycle (Kerstan 1995).

1.4.2: Feeding

Horse mackerel are zooplanktivorous. Small horse mackerel feed mainly on near-surface zooplankton (Crawford 1989), their dietary composition being similar to that of anchovy and sardine. On the other hand, large horse mackerel feed on large zooplankton such as polychaete worms, cumaceans, chaetognaths, a variety of crustaceans (including copepods, amphipods, euphausiids and decapods), squid and fish (Crawford 1989, Hecht 1990). The majority of adult horse mackerel in Namibia feed on euphausiids (Konchina 1986), and feed mainly in the afternoon (Andronov 1983, 1985, Konchina 1986). Their rates of food consumption and digestion time appear to be relatively rapid (Krzeptowski 1982, Andronov 1983, 1985).

Field studies investigating feeding periodicity, gut evacuation rate and daily ration of horse mackerel were conducted in South African waters by Pillar and Barange (1998). Copepods and euphausiids were found to be the main prey with the latter being the most common prey item on the South and West Coasts. The feeding studies by Andronov (1983, 1985) off Namibia and by Hecht (1990), Pillar and Barange (1998) off South Africa have provided useful baseline information on the types and relative quantities of prey consumed by horse mackerel. Their feeding habits were assessed by examining stomach contents of field-collected specimens, but quantitative feeding studies have yet to be undertaken under laboratory conditions.

1.5: Objectives of dissertation

The objective of this study was to examine various aspects of the feeding of horse mackerel through laboratory experiments conducted on captive specimens. The experiments investigated the effects of prey particle size and concentration on feeding behaviour, selectivity and rates of consumption of prey by horse mackerel. The hypothesis that horse mackerel are size selective feeders was tested by laboratory experiments. The experimental approach was similar to that used by van der Lingen (1994) for sardine, i.e. feeding the fish a variety of food types of different sizes and monitoring their feeding behaviour and clearance rates. The information presented will complement field data by Pillar and Barange (1998) concerning the feeding habits of this species.

The dissertation consists of five chapters. The second chapter describes the methods used in laboratory feeding experiments. Chapters 3 and 4 present results on the feeding behaviour, selectivity and clearance rates of large and small juvenile horse mackerel, respectively. The last chapter discusses the results obtained and compares the feeding behaviour of horse mackerel with those of sardine and anchovy in the southern Benguela ecosystem.

CHAPTER 2

MATERIALS AND METHODS

2.1: Fish collection and maintenance

This study was carried out at the Marine and Coastal Management Research Aquarium in Sea Point, Cape Town. Juvenile horse mackerel were collected in Kalk Bay Harbour using a dip–net and then transported to the aquarium in 450 l black plastic drums containing continuously aerated seawater. On arrival, they were transferred to experimental 12 000 l tanks supplied with 18-µm filtered sea-water. Air was supplied through a porous airline around the circumference of the tank. Water temperature ranged between 12.5^{0}C and 20^{0}C. Horse mackerel were acclimated for a period of one to three months to laboratory conditions before being used in experiments. The fish were fed once a day on grated frozen sardine, or frozen euphausiids and frozen mixed copepods when available.

2.2: Experimental procedure

Two groups of fish were used in the experiments, large and small juveniles. Large juveniles (131.8 ± 11.0 SD mm *TL*) were collected in February 1999 and grew to 183.5 ± 8.2 *TL* mm by the end of experiments in December 2000. Small juveniles (90.0 ± 8.2 mm *TL*) were collected in January 2001 and the experiments were conducted until May 2001.

The prey items used in the experiments consisted of a variety of natural zooplankton (Table 2.1), including crustacean eggs and nauplii, cladocerans, harpactacoid copepods, cyclopoid copepods, small copepods, calanoid copepods, tunicates and mysids, which were collected on the same day as the experiment. The zooplankton was collected in bays around Cape Town (Granger Bay, Table Bay, Millers Point and Hout Bay) using a 200 - μm mesh drift net.

Table 2.1: Summary of experimental food types used.

Food Organisms	
PREY CATEGORY	**PREY TAXA**
Crustacean nauplii	Cirripede nauplii.
	Copepod nauplii
Crustacean eggs	Copepod eggs
Cladocerans	*Evadne* spp.
	Podon spp.
	Penilia spp.
Harpactacoid copepods	Harpactacoids
Cyclopoid copepods	*Oithona* spp.
	Oncaea spp.
Small copepods	*Paracalanus* spp.
	Clausocalanus spp.
	Ctenocalanus spp.
	Parvocalanus spp.
Calanoid copepods	*Calanus* spp.
	Calanoides spp.
	Centropages spp.
	Acartia spp.
Decapod zoea larvae	Decapod zoea larvae.
Chaetognaths	Chaetognaths
Mysids	Mysids spp.
Tunicates	*Oikipleura* spp.
Polychaetes	Polychaete larvae
Echinoderms	Echinoderm larvae

Mixtures of prey types and size-classes were used in experiments in order to examine feeding behaviour, assess whether horse mackerel select their prey on the basis of size and estimate their clearance rates. In addition, in some experiments monocultures of mysids were used as the prey organism. Whilst mysids have not been reported in the diet of the juvenile horse mackerel, they were used in the experiments because of their similar size and appearance to euphausiids, a major prey item of juvenile horse mackerel. Euphausiids were not easily collected and mysids were used instead. Experiments consisted of introducing prey assemblages into the tanks with experimental fish and observing their feeding response.

Prior to each experiment, the fish were starved for a period of one to three days to standardize their hunger state. A porous air tube around the perimeter of the inside of the tank provided a continuous fine bubble curtain. The day before an experiment the sides and the bottom of the tanks were scrubbed and the dirt was siphoned out of the tank. This procedure was repeated before the start of the experiment. Prior to the experiment, the volume of the water in the tank was reduced (depending on the density of food and number of fish in the tank) and the water and air supply were cut off. Prior to introduction of food into the tank, a video camera that was positioned 3 meters above the tank was switched on to record the activity of the fish and left running for the duration of the experiment. Experiments were always conducted under artificial light of the same intensity. The floor of the experimental tank was marked with grid lines 10-cm apart, in order to provide reference positions against which fish swimming speed could be

measured. Non-feeding swimming speed was recorded for ± 15 minutes, after which food was introduced into the tank and the bubble curtain was activated for three minutes to ensure thorough mixing. In all experiments fish started feeding immediately after the introduction of food. The food concentration in the tank was determined by sub - sampling immediately (t = 0) after the bubbling curtain was discontinued. Thereafter, subsamples were taken at 15minute intervals until feeding had ceased, or the food was depleted to negligible concentrations. A clear perspex tube (10.5-cm internal diameter), which mated with 120μm mesh-bottomed cups placed randomly on the bottom of the tank, was used for sampling. For each subsample, the tube was mated to each cup and withdrawn from the tank with the zooplankton concentrated on the mesh. After each subsample collection, the cups were replaced in the tank.

Using a clear perspex tube for sampling minimized disturbance of the fish because of its relative invisibility in the water, and the small volume taken per subsample (between 2.68 and 3.90 l) did not reduce the volume of water in the tank substantially. Food particles collected from the mesh were transferred into small sampling jars and preserved in 5% formalin for later examination. A total of 10 subsamples were taken at each sampling interval

2.3: Data analysis

2.3.1: Prey concentration and size distribution

The number of prey items in each subsample were counted, and prey were identified to genus where possible. Because of the difficulty in identifying *Paracalanus* spp., *Ctenocalanus* spp., *Clausocalanus* spp. and *Parvocalanus* spp., these calanoid copepods were listed as "small copepods".

Means and standard deviations of both total prey concentration and the concentration of individual genera were calculated at each time interval within each experiment. Significant differences between means measured at subsequent time intervals during the course of an experiment were calculated using one–way ANOVA/Tukey multiple range tests or Kruskal–Wallis/Newman–Keuls tests, depending on homogeneity of the variances. Statistical significance was accepted at the $p < 0.05$ level. At each sampling interval, mean prey size and prey size frequency distributions were determined by measuring 50 individual prey items from each subsample using a dissecting microscope fitted with a micrometer. The size frequency data were normalized using an arcsine transformation:

$$p' = \text{arcsine } p^{1/2} \qquad \text{.....(2.1)}$$

where p is the original proportion and p' is the transformed proportion. This transformation is used when percentages are small or large (i.e. 0-30% and 70-100%), so that the resultant data will have an underlying distribution that is nearly normal (Zar 1999). The nutritional value of prey items was estimated using relationships relating dry

mass and carbon content to size provided by van der Lingen (1999). Size frequency distributions, and the distribution of carbon within size classes, were plotted for each sampling interval within each experiment (Table 2.2).

Table 2.2: Classification scheme, taxa, measurements taken, morphometric relationships, and equations used to calculate the dry mass and carbon content of zooplankton used in the horse mackerel experiments. Length measurements are in μm and dry mass is in μg, except where indicated otherwise. TL and PL are total and prosome length respectively, and DM is dry mass (van der Lingen 2002).

PREY CATEGORY	TAXA	MEASUREMENTS TAKEN AND MORPHOMETRIC RELATIONSHIPS	DRY MASS (DM) CALCULATIONS	CARBON CONTENT
Calanoid Copepods	*Calanus* *Calanoides* *Centropages* *Acartia*	TL or PL All genera TL = 1.198*(PL)+52.4	Ln (DM) = 2.74*ln(PL)-16.41	0.424*DM
"Small copepods"		TL or PL All genera TL= 1.132*(PL)+120.1	Ln (DM) = 2.74*ln(PL)-16.41	0.424*DM
Cyclopoid copepods	*Oithona* *Oncaea* *Corycaeus* *Copilia*	TL or PL TL = 1.684*(PL)+35.8 TL = 1.367*(PL)+11.3 As for *Oncaea* spp.	Ln (DM) = 1.96*ln(PL)-11.64	0.424*DM
Harpacticoid copepods		TL	Ln (DM) = 1.96*ln(TL)-11.64	0.424*DM
Cladocerans	*Evadne* *Podon* *Penilia*	TL	DM $= 3.946*(TLmm)^{2.436}$	0.424*DM
Crustacean eggs		Diameter (Ø)	Ln (DM) = 0.0143*(Ø)	0.400*DM
Crustacean nauplii	Copepod nauplii Cirripede nauplii	TL	$DM = 80.627*TL^{4.27}$	0.424*DM
Mysids		TL	DM (mg) $= 0.0012*TL\ (mm)^{3.16}$	0.424*DM

2.3.2: Clearance rates

Consumption rates of zooplankton prey by juvenile horse mackerel were investigated through the estimation of clearance rates (F), defined by James and Findlay (1989) as the volume from which food particles are removed per unit time. Significantly different food concentrations for each time interval within each experiment were used to calculate the clearance rate using the formula of Harvey (1937 in van der Lingen 1994):

$$F = \frac{v * (\ln C_i - \ln C_f)}{N * \Delta t} \qquad \text{.....(2.2)}$$

where F is the clearance rate (l fish^{-1} min^{-1}), v is water volume (l), C_i and C_f are food concentrations at time i (initial) and time f (final) respectively (no. of food particles l^{-1}), Δt is the time interval between i and f (minutes) and N is the total number of fish in the tank.

Clearance rates estimated for each time interval were plotted against mean particle size for that interval to assess the hypothesis that juvenile horse mackerel feed by selecting large particles over small ones. Similarly, F was plotted against mean prey concentration (<C>) in order to examine the effect of prey concentration on the feeding behaviour. Mean prey concentrations were calculated from the formula of Seale and Beckvar (1980), cited by van der Lingen (1994):

$$< C > = \frac{C_f - C_i}{\ln(C_f / C_i)} \qquad \text{.....(2.3)}$$

where <C> is the mean concentration (number l^{-1}).

2.3.3: Feeding behaviour and swimming speed

The behaviour of the fish before and during feeding was recorded by means of a video camera recording at 25 frames. s^{-1} throughout the experiment. Each video was analysed frame-by-frame to determine swimming speeds as well as examine feeding behaviour. Swimming speeds were estimated by counting the number of frames taken by individual fish to cross one grid line completely, and were expressed as body lengths per second (BL s^{-1}). A total of 50 measurements of swimming speed was taken between each 15-minute time interval and only fish whose paths did not deviate by more than approximately 20^0 from their original direction during the period of counting were considered. Swimming speeds were plotted against time interval, against particle size, and against prey carbon concentration for food particles in order to quantify the effects these parameters had on fish behaviour.

CHAPTER 3
LARGE JUVENILE HORSE MACKEREL: FEEDING BEHAVIOUR, SELECTIVITY AND CLEARANCE RATES

Eight experiments were conducted to investigate the feeding behaviour, selectivity and rate of consumption of crustacean zooplankton by large juvenile horse mackerel ca. 150-200 mm in length. Detailed results shown are from two experiments in order to illustrate in detail the changes in fish behaviour, and zooplankton concentration composition and size distribution during the course of an experiment. The first experiment illustrated below (Expt. 4) used an assemblage of mixed copepods as prey and the second experiment (Expt. 8) describes results obtained for mysids, which form a single, large prey type (Table 3.1). Combined results of all experiments are also presented to illustrate the feeding behaviour of large juvenile horse mackerel

3.1: Feeding behaviour.

Although horse mackerel appeared to select a single prey at a time, several prey can be sucked into the mouth accidentally during capture of the targeted item. These fish have protrusible mouths and during feeding they shoot out their lips, and open their mouths to suck in the water and the prey. Particulate feeding is characterized by opening and closing of the mouth, accompanied by flaring of the opercula, sucking the prey and the surrounding water into the mouth and swallowing (Lazzaro 1987). When the mouth opens, the buccal cavity expands, which creates a negative pressure that draws the prey into the mouth propelled by a current of water. The water exits through the flared operculae after prey capture. No other type of feeding behaviour was observed.

Table 3.1. Large juvenile horse mackerel: summary of experiments, showing the number of fish, starvation period, fish size, duration of each experiment, prey type and size, and water temperature for each feeding experiment performed.

Experiment number	No. of fish	Starvation time (days)	Fish size, (TL, ± SD, mm)	Duration (minutes)	Prey type	Prey size (µm)	Temp (^{0}C)
Large juveniles							
1	19	1	167.8 ± 13.3	40	Mysids	6141. 0± 913.0	16.5
2	19	2	No video	40	Mixed copepods	1302.6 ± 464.4	20.0
3	19	3	171.9 ± 28.3	60	Mixed copepods	1249.5 ± 391.7	16.5
4	19	2	172.1 ± 15.9	60	Mixed copepods	1016.2 ± 343.3	16.0
5	19	1	175.7 ± 16.7	60	Mixed copepods	886.3 ± 343.3	17.0
6	19	3	182.0 ± 19.6	60	Mixed copepods	987.7 ± 387.2	16.5
7	19	1	182.7 ± 11.5	75	Mixed copepods	1038.7 ± 295.2	12.3
8	19	2	183.5 ± 8.2	60	Mysids	9441.7 ± 1869.6	17.0

3.1.1: Expt. 4. mixed copepods

Large juvenile horse mackerel swam in a tight shoal at an average speed of 0.49 ± 0.08 body lengths per second ($BL.s^{-1}$) before the introduction of food into the tank, (Fig. 3.1). Sometimes they exhibited startled responses to disturbances such as noise near the tanks. When food was introduced into the tank, the fish initially broke up the shoal, increased their swimming speeds and immediately start to feed. Swimming speeds increased significantly ($p < 0.05$) to 1.30 ± 0.18 $BL.s.^{-1}$(Fig. 3.1), with the fish changing direction frequently. As food concentrations became depleted during the experiment, the fish decreased their swimming speeds and swam at a speed close to that of non–feeding levels (Fig. 3.1).

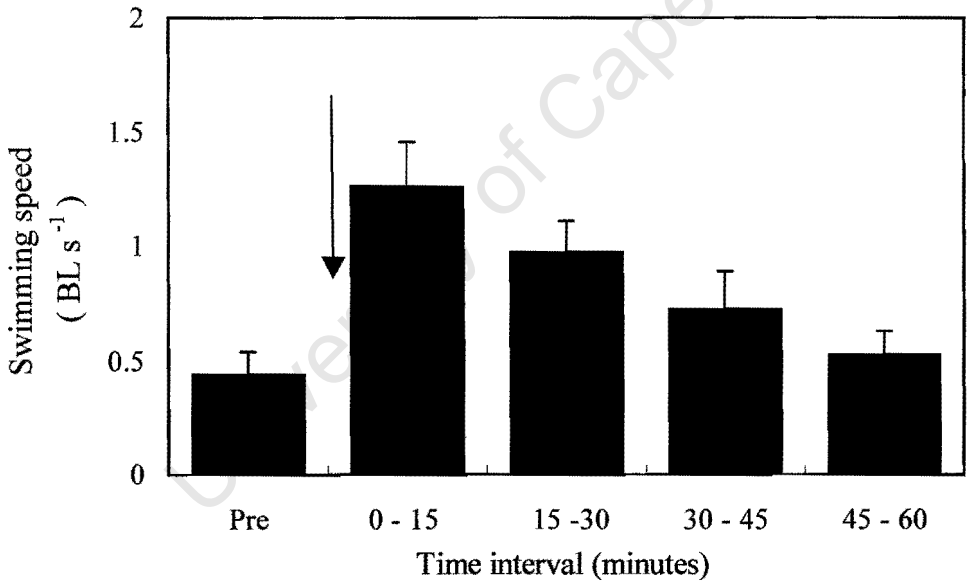

Fig. 3.1. Large juvenile horse mackerel: mean swimming speeds (+ 1SD) during Expt. 4 at different time intervals before and after food was introduced into the tank. The arrow shows when food was introduced.

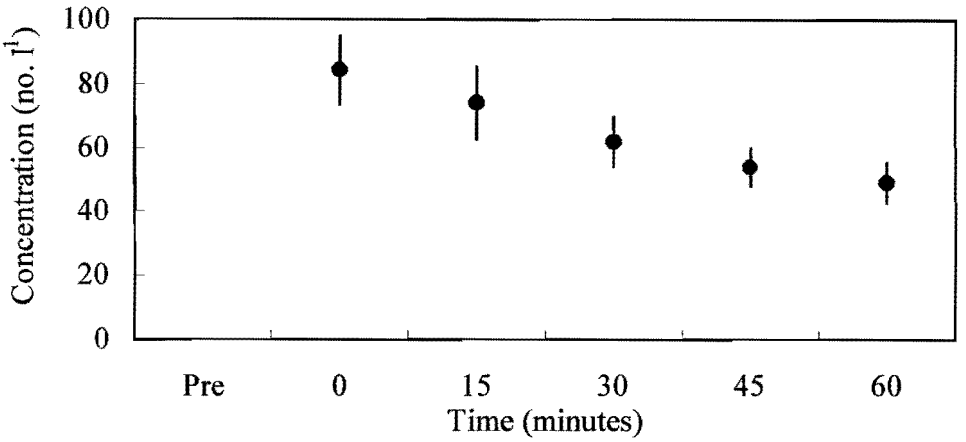

Fig. 3.2: Large juvenile horse mackerel: prey concentration (mean ±2SD) as a function of time after food was introduced into the tank during Expt. 4.

A rapid decrease in food concentration with time was evident between the time intervals after food had been introduced into the tank (Fig. 3.2). Prey items used in Expt. 4 were small and large zooplankton ranging from 0.2 to 2.8 mm, dominated by prey of 0.8–1.4 mm at t=0 (Fig. 3.3). During the course of the experiment, food particles of between 1.6 and 2.8 mm were depleted rapidly, and at the end of the experiment, (t = 60), only small prey of 0.2–1.4 mm remained. The results clearly show that horse mackerel are selective feeders, preferentially removing large prey particles.

At the beginning of Expt. 4, the prey assemblage was made up of mixed copepod species primarily *Acartia* (36%), *Oithona* (31%), *Calanus* (8%), *Calanoides* (6%), small copepods (6%) and "others" (13%), such as *Centropages, Oncaea,* Harpacticoids, and copepod eggs. By the end of the experiment, large prey such as *Calanus* and *Calanoides* had almost disappeared completely, and only small zooplankton prey items remained. (Fig. 3.3).

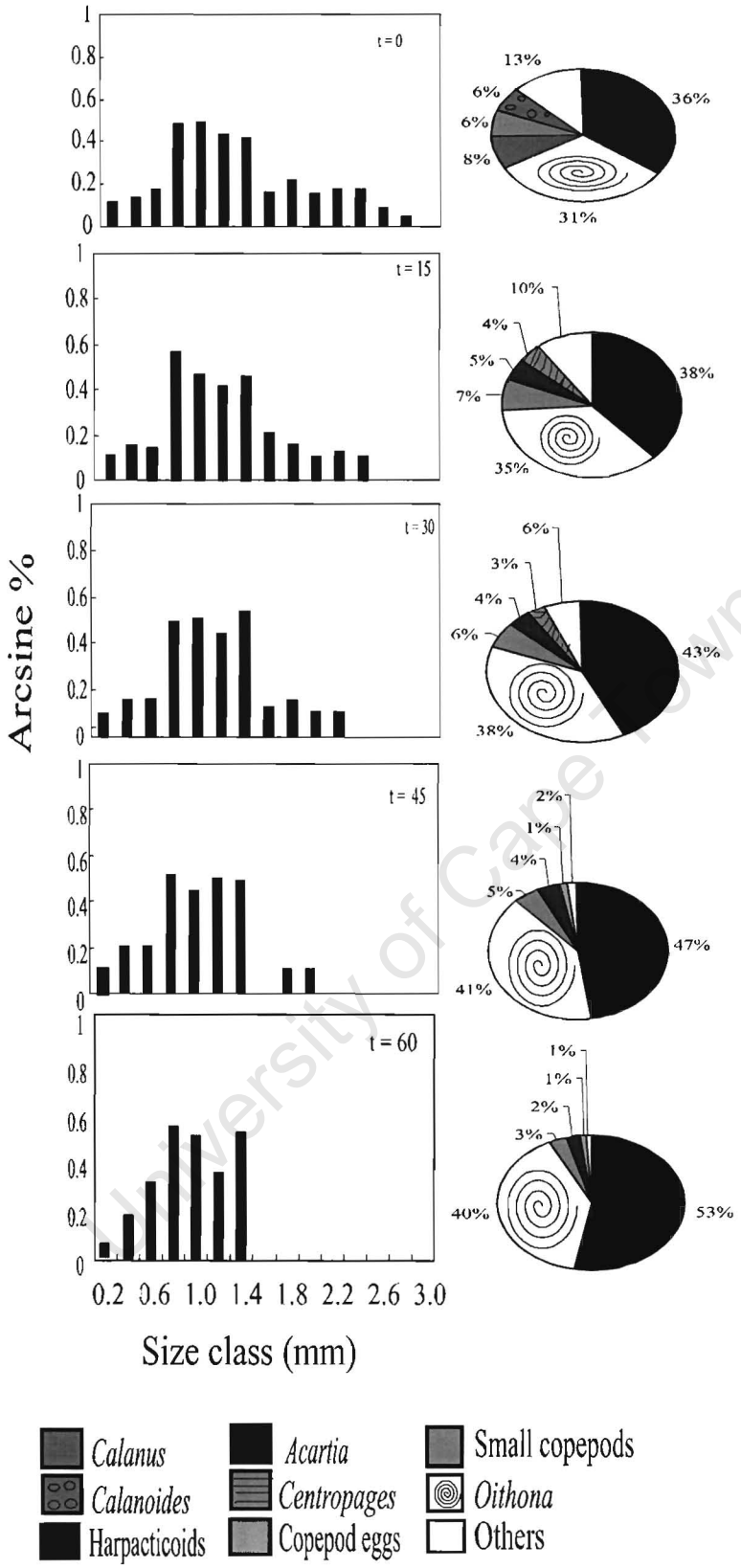

Fig. 3.3. Large juvenile horse mackerel: size frequency distribution and composition of prey used in Expt. 4 at various time intervals after food was introduced into the tanks.

The rapid reduction with time of large prey types such as *Calanus* and *Centropages*_and the relative increase in the proportions of *Acartia* and *Oithona* indicate that horse mackerel were selecting large prey types and confirm the results suggested by the size frequency histograms.

Fig. 3.4 shows that the concentration of large calanoid copepods decreased rapidly with time; their concentration differed significantly between time intervals [*Calanus,* (one – way ANOVA, $F = 47.80$, $df = 4, 45$, $p < 0.005$) and *Centropages* (one – way ANOVA, $F = 42.40$, $df = 4, 45$, $p < 0.005$)].

All the concentrations of small prey items (e.g. *Oncaea)* decreased with time, but not as fast as calanoid copepods (Fig. 3.4). Their concentrations differed significantly with time, especially in small copepods such as *Oncaea* (one – way ANOVA, $F = 35.85$, $df = 4, 45$, $p < 0.005$) and *Oithona* ($F = 10.21$, $df = 4, 45$, $p < 0.005$).

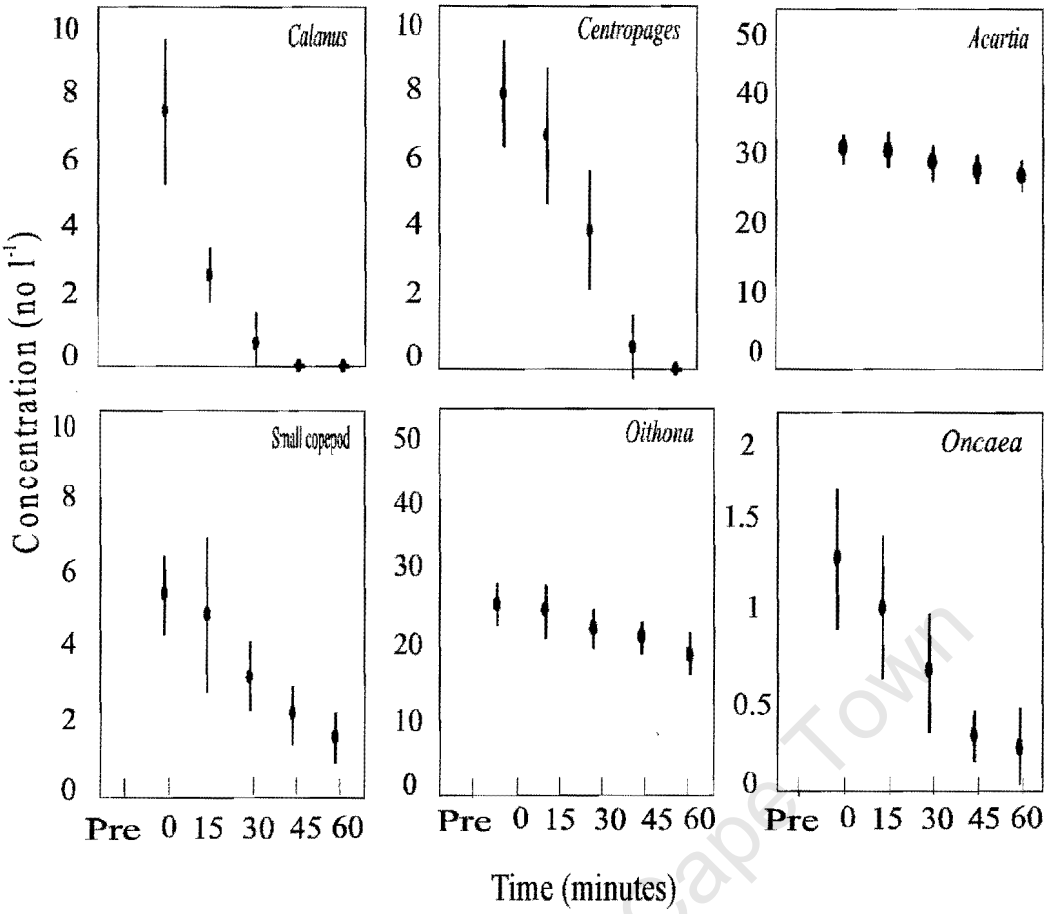

Fig. 3.4. Large juvenile horse mackerel: concentration (mean ± 2SD) of the various prey species as a function of time after introduction of food into the tank during Expt. 4. Panels ordered by prey size.

Prey >1.5 mm were removed more rapidly than smaller <1.5 mm prey. The concentrations of the prey between successive time intervals were significantly different (one-way ANOVA, $p < 0.05$) (Fig. 3.5). The concentrations of the large prey (> 1.50mm) in the experiment showed more highly significant differences ($p < 0.05$) statistically than the small ones (< 1.5 mm) (Table 3.2).

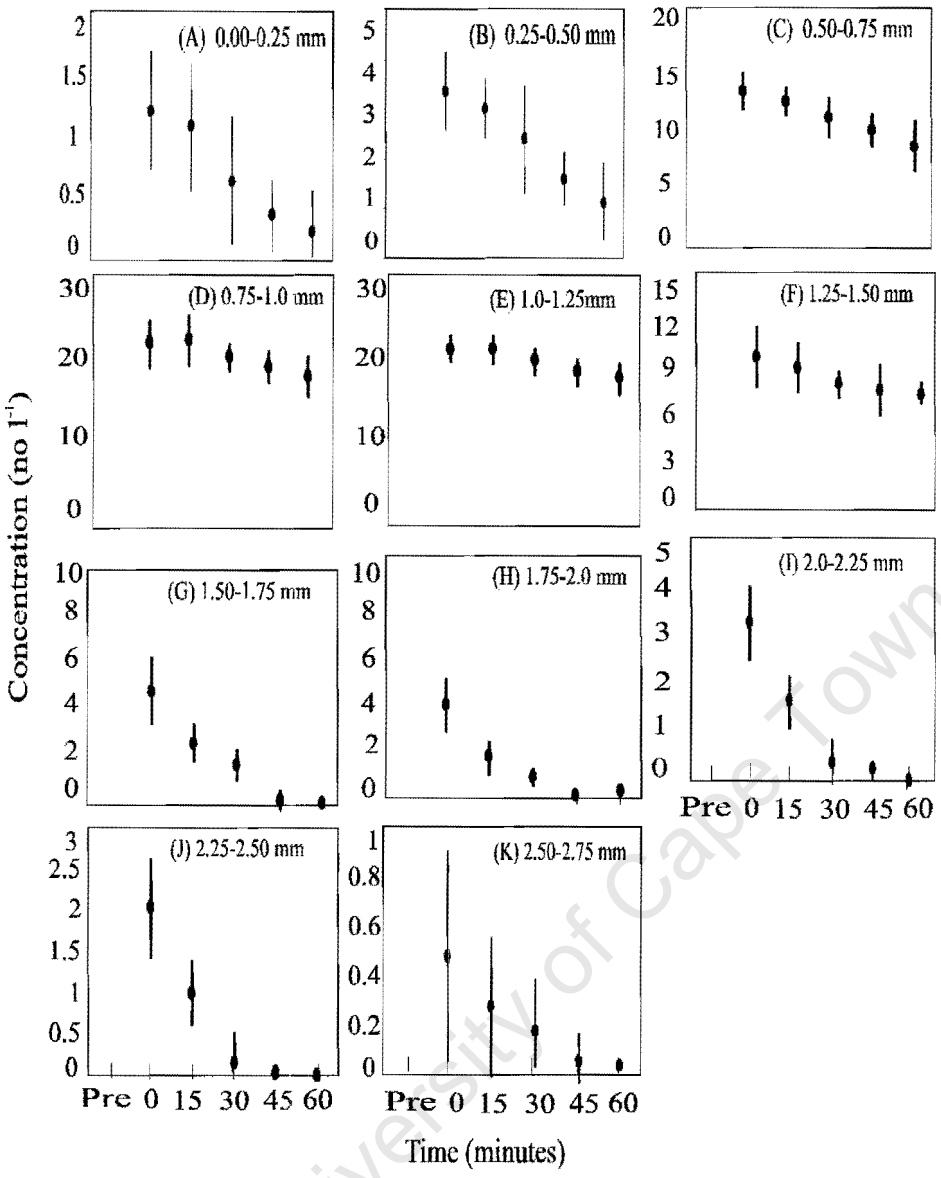

Fig. 3.5. Large juvenile horse mackerel: concentration (mean ± 2SD) of the various prey sizes as a function of time after introduction of food into the tank (Expt. 4).

Table 3.2. Feeding of large juvenile horse mackerel: One – way ANOVA of concentrations (no. l^{-1}) of different size classes of mixed copepods.

Size class (mm)	F values	df	p-value
0.0-0.25	6.42	4, 45	<0.01
0.25-0.50	15.51	4, 45	<0.01
0.50-0.75	15.85	4, 45	<0.01
0.75-1.0	6.05	4, 45	<0.01
1.0-1.25	4.18	4, 45	<0.01
1.25-1.50	4.21	4, 45	<0.01
1.50-1.75	43.81	4, 45	<0.001
1.75-2.0	45.74	4, 45	<0.001
2.0-2.25	46.13	4, 45	<0.001
2.25-2.50	43.06	4, 45	<0.001
2.50-2.75	17.97	4, 45	<0.001

When the prey particles were converted to their carbon equivalents, large copepods were expected to contribute a greater proportion of carbon to the diet than the small zooplankton. Although the samples were dominated by the small prey, the carbon contents of large zooplankton were the most utilized by the fish (Fig. 3.6). With time, carbon was observed becoming concentrated in small-size classes, similar to the trend found in Figure 3.3. For example, small copepods such as *Oithona* were found in all samples and were numerically dominant. Large copepods such as *Calanus* and

Centropages, which had high carbon content, were encountered at the beginning of the experiment, but very few remained at the end.

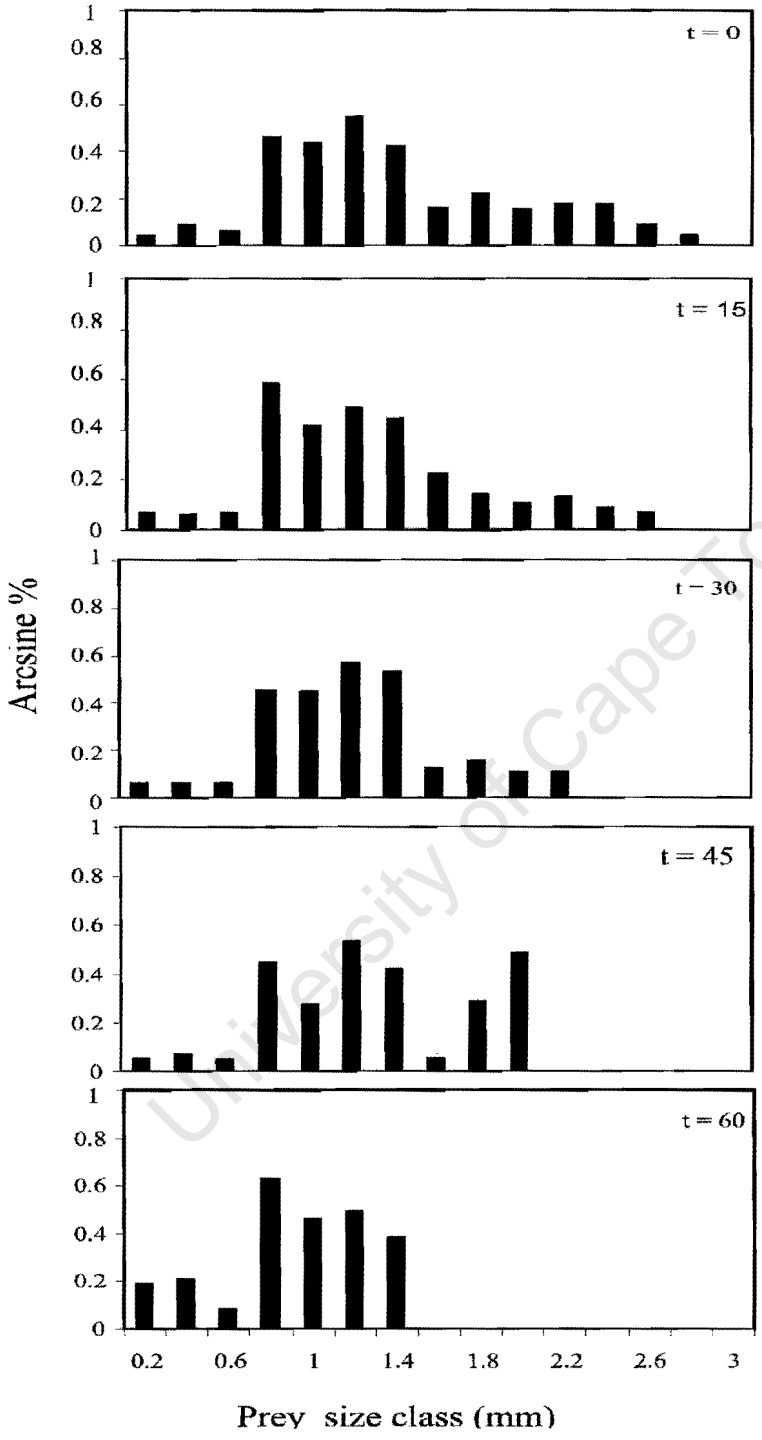

Fig. 3.6. Large juvenile horse mackerel: distribution of carbon content (% of mg l^{-1}) by size class of prey organisms sampled at 15 minute time intervals for Expt. 4.

3.1.2. Expt. 8: mysids

In addition to using mixed prey assemblages that were comprised of a wide range of prey types and size, similar experiments were carried out using a single, large prey type, i.e. mysids. Whereas mysids do not occur in the diet of juvenile horse mackerel they are similar in size and appearance to euphasiids, a dominant prey item. However, because of the difficulties encountered collecting euphasiids for experiments, mysids were used as 'surrogate' euphasiids.

Results obtained show that large juvenile horse mackerel behaved in a manner similar to that shown in Fig. 3.1, increasing their swimming speeds from an average of 0.39 ± 0.05 $BL.s^{-1}$ when not feeding to 1.69 ± 0.30 $BL.s^{-1}$ at the beginning of the experiment (t=0) and later decreased their swimming speeds with time (Fig. 3.7).

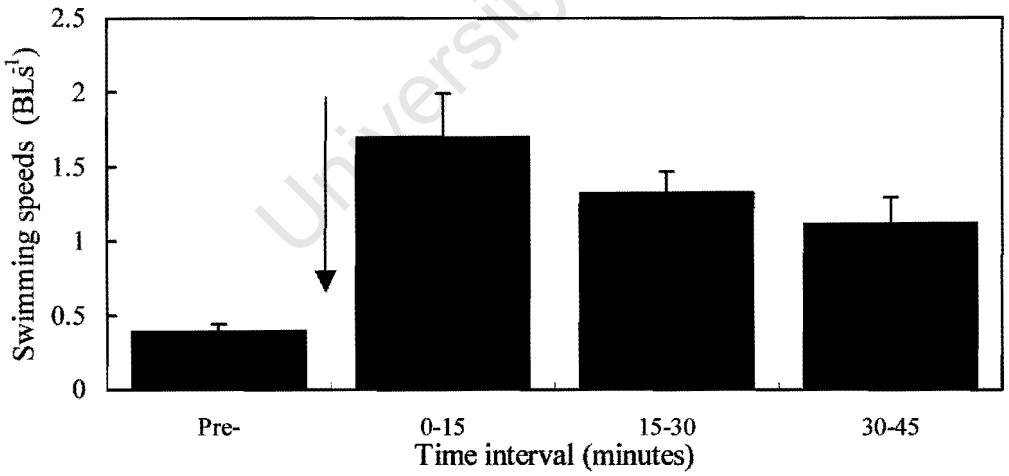

Fig. 3.7. Large juvenile horse mackerel: mean swimming speeds (+ 1SD) during Expt. 8 at different time intervals before and after food was introduced into the tank. The arrow shows when food was introduced.

Mysid concentrations in most size-classes decreased significantly ($p < 0.05$) with time (Table 3.3). The exception was the 10.5-12.0 mm mysid size class, possibly because the prey of that size were very sparse in the tank (Fig. 3.8).

Table 3.3. Feeding of large horse mackerel: Statistical parameters for concentration (no. l^{-1}) of different size classes of mysid between time intervals.

Size class (mm)	F values	df	p-values
6.0-7.5	25.58	3, 36	<0.0001
7.5-9.0	34.58	3, 36	<0.0001
9.0-10.5	22.8	3, 36	<0.0001
10.5-12.0	3.28	3, 36	>0.05

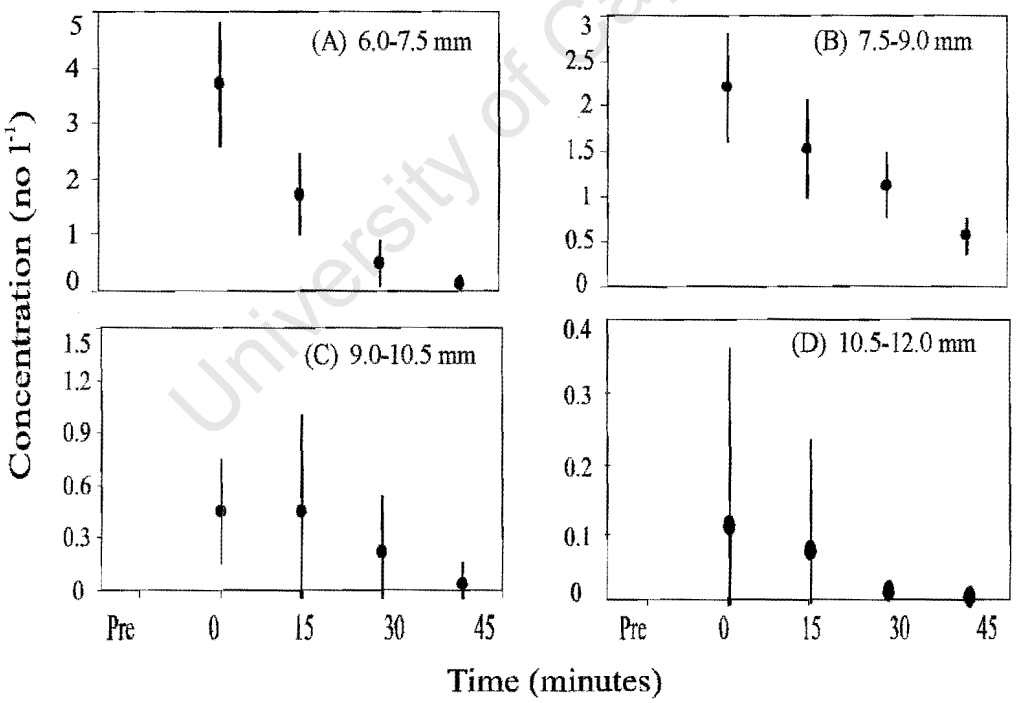

Fig. 3.8. Large juvenile horse mackerel: mean concentration (± 2SD) for mysid size classes as a function of time (minutes), Expt. 8.

Frequency distribution histograms show the size distribution at t=0 to be ranging from 6.0 to 15mm but at the end (t=45) the distribution was from 9-12mm. The prey size classes showed varying prey depletion in different size classes (e.g. <10.5 and > 10.5mm, Fig. 3.9).

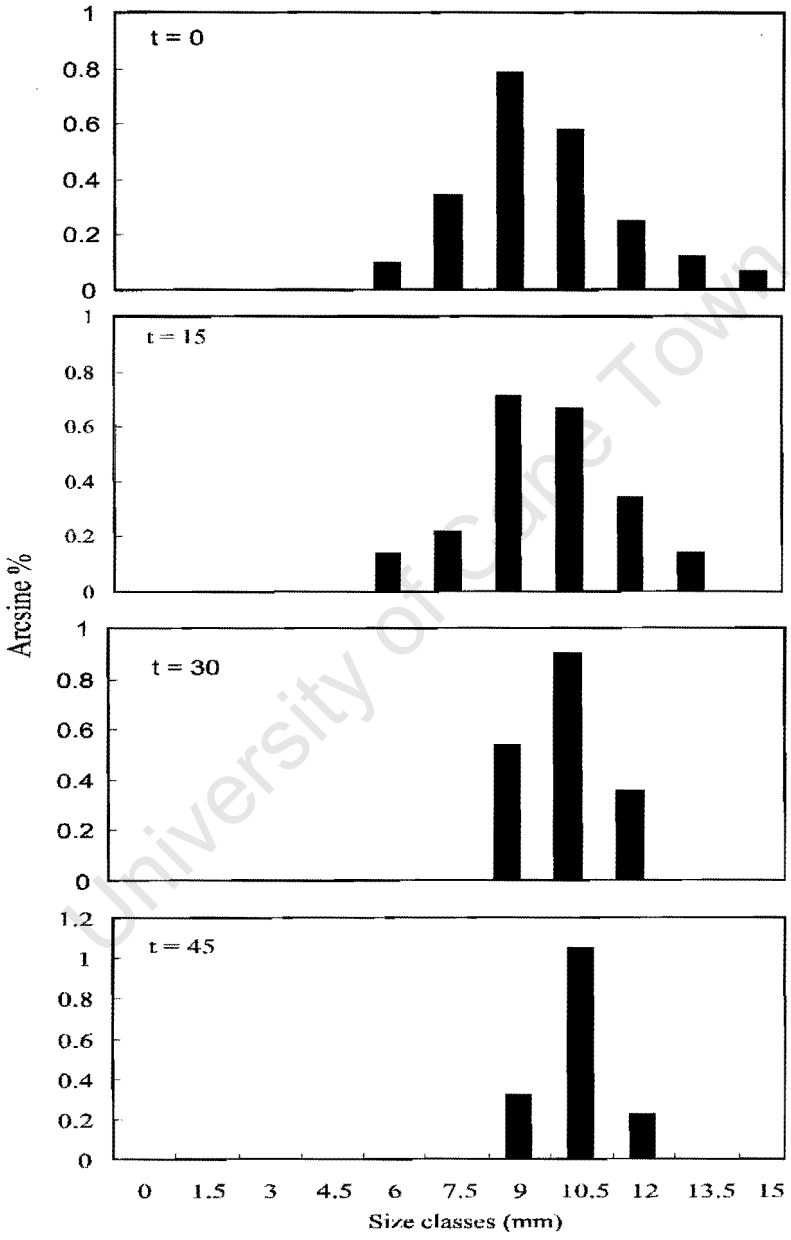

Fig. 3.9. Large juvenile horse mackerel: size frequency distribution of mysids at different time intervals after food was introduced into the tank during Expt. 8.

The carbon contribution for mysids (Fig 3.10), showed a pattern similar to that of their size distribution (Fig 3.9). All size classes were removed irrespective of size.

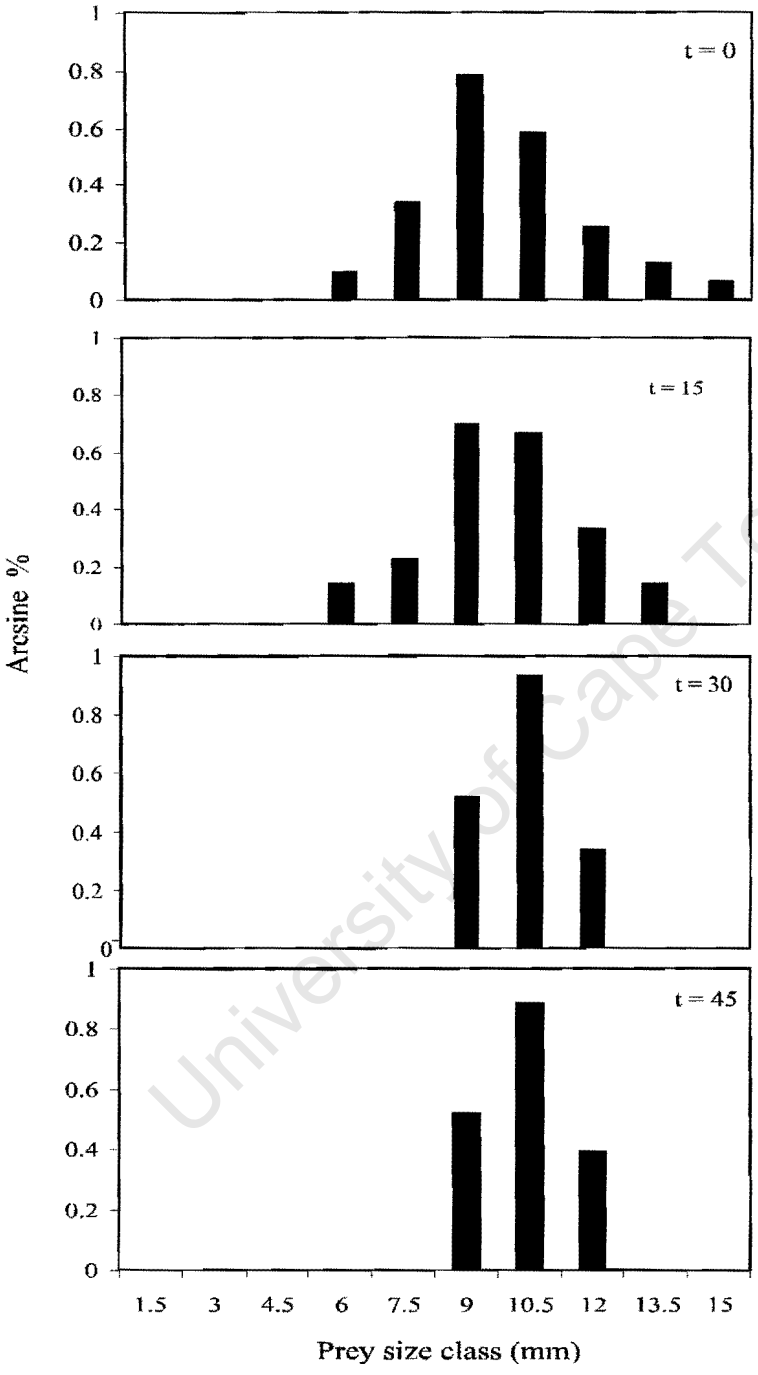

Fig. 3.10. Large juvenile horse mackerel: frequency distribution of carbon content (% of mg l^{-1}) by size class of mysids sampled at 15 minute time intervals for Expt. 8.

3.2: Combined results: effects of prey size and/or concentration on fish swimming speeds.

Large juvenile horse mackerel behaved differently in the absence and presence of food, increasing their swimming speeds markedly compared to non-feeding levels after food had been introduced into the tank. Scatterplots of swimming speeds as a function prey size and prey concentration (Fig. 3.11) indicated that both of those parameters appeared to influence fish swimming speed.

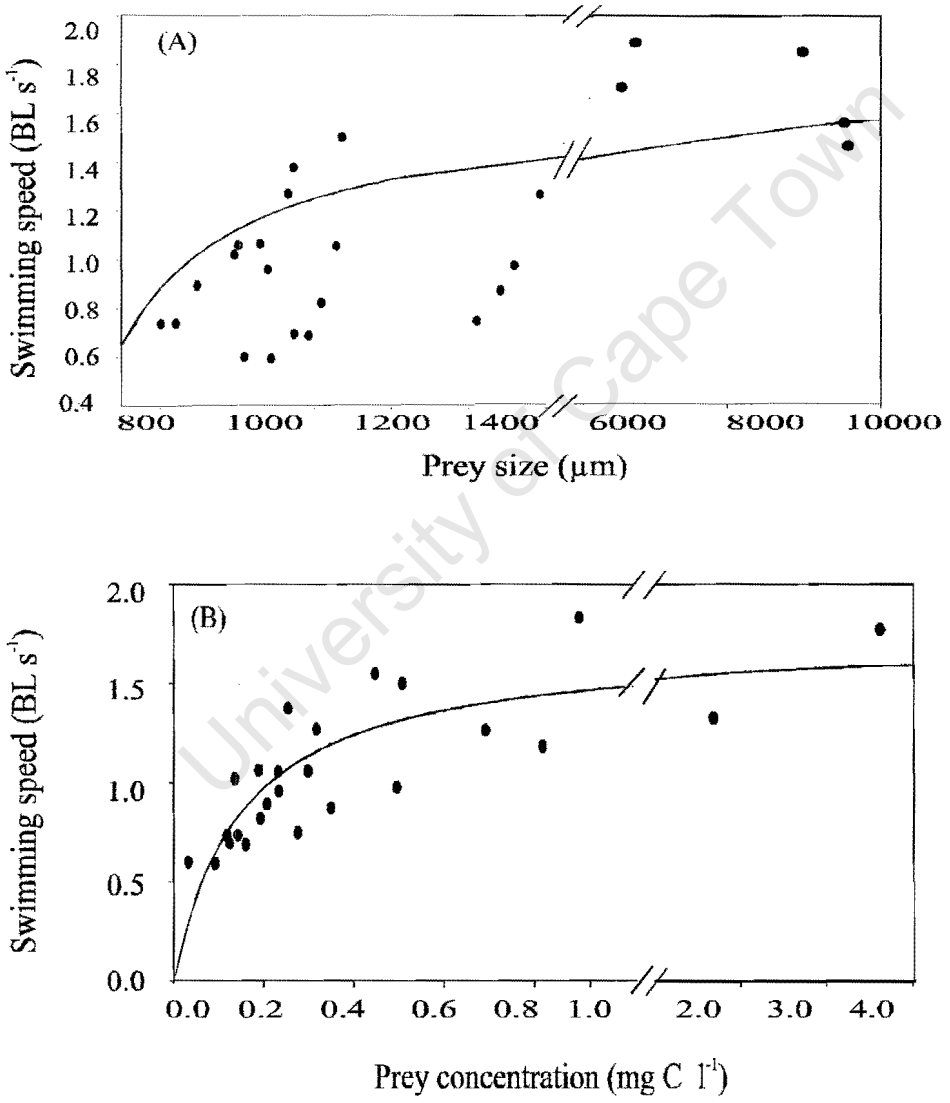

Fig. 3.11. Effect of (A) prey size and (B) prey concentration on the swimming speed of large juvenile horse mackerel

In both cases, swimming speeds increased asymptotically towards a maximum value, and the relationships can be described using hyperbolic functions:

$$\text{Swimming speed} = \frac{1.68 * \text{prey size}}{802.14 + \text{prey size}}, (r^2 = 0.47, n = 24\ p < 0.0001) \quad \text{.....(3.1)}$$

$$\text{Swimming speed} = \frac{1.68 * \text{prey concentration}}{0.15 + \text{prey concentration}}, (r^2 = 0.62, n = 24, p < 0.0001) \quad \text{...(3.2)}$$

3.3: Clearance rates

Clearance rates of large juvenile horse mackerel varied with particle size. Small food particles ranging from 0.50 to 1.50 mm were removed at very low clearance rates of between 1.45 – 5.90 l fish^{-1} min.$^{-1}$, whereas large food particles of 1.50 - 9.0 mm had higher clearance rates, i.e. up to 23.85 l fish^{-1} min.$^{-1}$. There were some exceptions to this trend, where large prey had slower clearance rates than expected e.g. prey > 9.0 mm were removed at rates of < 15 l fish^{-1} min.$^{-1}$, (Fig. 3.12). Clearance rates (F) increased with prey size (x) to a predictable maximum size, using a sigmoid curve to describe the relationship, the sigmoid curve gave a better fit when compared to other functions that were fitted on the data.

$$F = 3.18 \frac{7.05}{(1 + \exp\ (-(x-1.74)/0.023)}, (r^2 = 0.34, n = 77, p < 0.0001) \quad \text{.....(3.3)}$$

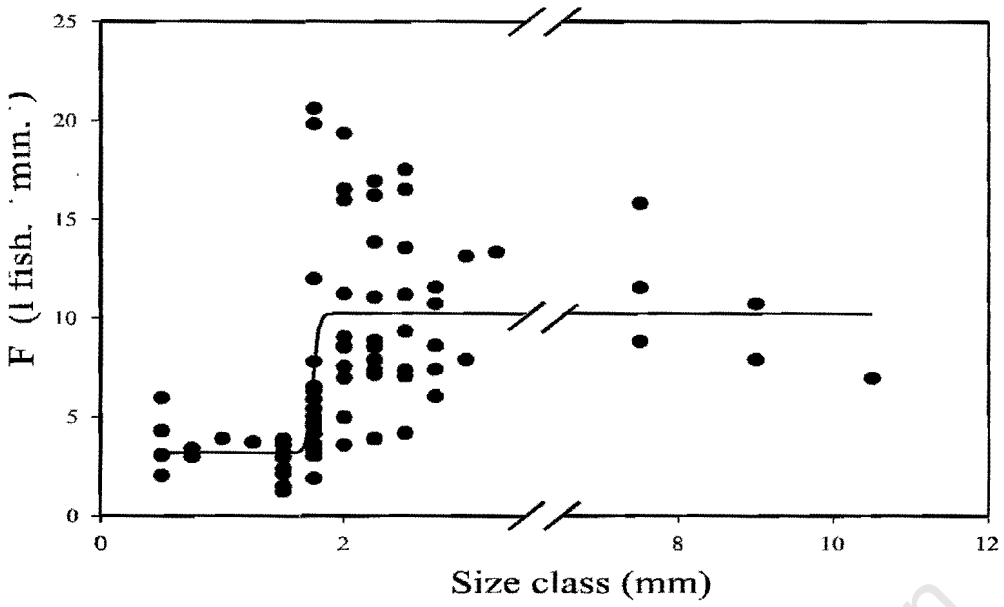

Fig. 3.12. Clearance rate (F) of large juvenile horse mackerel as a function of prey size.

Because in all experiments, food concentration decreased with time, clearance rates were plotted as a function of time, in order to examine whether F (clearance rates) remained constant throughout the experiments. Fig. 3.13A, shows that at the initial stages of an experiment, i.e. between 0-15 minutes, fish appeared to feed on almost all the prey organisms they encountered, with clearance rate values for different food types being very similar. After that initial time interval, the fish started to select certain prey types, as evidenced by increased clearance rates on large prey such as *Calanus* and *Calanoides*. For an example a considerable increase in the clearance rate of e.g. *Calanus* from 10 to 23 l fish^{-1} min.$^{-1}$ was seen after the first 15 minutes compared to small zooplankton, e.g. *Oncaea* and Harpacticoid, which ranged between 2.0–10.0 l fish^{-1} min.$^{-1}$. This could be attributable to fish becoming more aware of the presence of large individuals among the prey (i.e. learned behaviour) or the decrease in prey concentration could have made it

easier for fish to preferentially remove particles from the water. Fig. 3.13B shows that clearance rate (F) is inversely proportional to concentration (conc), the relationship best described by an exponential decay curve:

$$F = 15.59\, e^{-0.133\, conc} \quad (r^2 = 0.46, p < 0.05), \qquad \text{.....(3.4)}$$

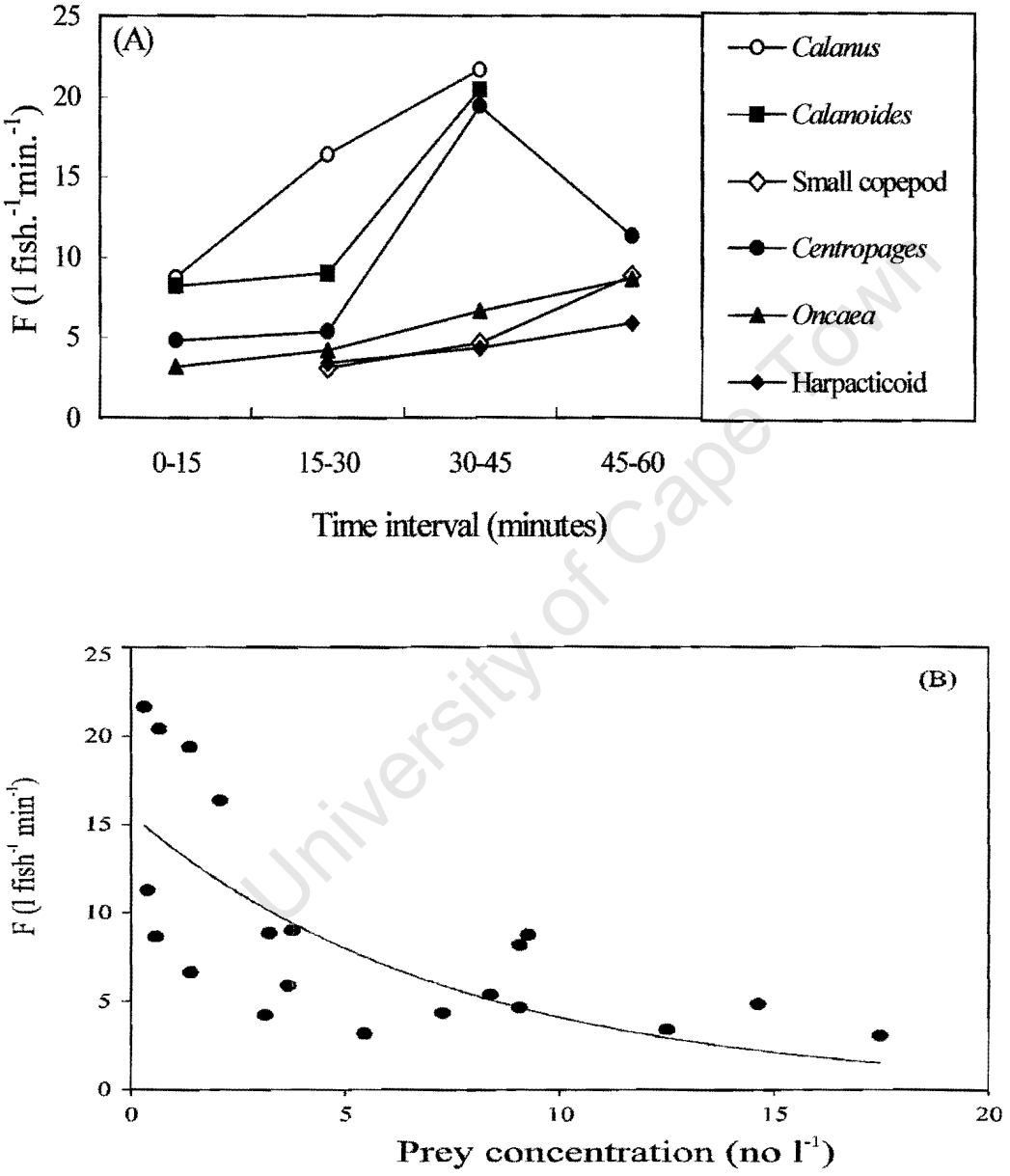

Fig. 3.13. (A) Clearance rate (F) as a function of time interval, and (B) as a function of prey concentration for Expt. 8.

In summary it is clear that horse mackerel select their prey preferentially. Larger prey were positively selected and hence cleared faster than the smaller ones, and the relationship between clearance rate and prey size is best described by a sigmoid curve with a marked increase above 1.8 mm. Swimming speeds of large juveniles increased during feeding, and were proportional to both particle size and prey carbon concentration. Clearance rates increased with time, up to a maximum after about 30-45 minutes feeding on larger copepods such as *Calanus*, *Calanoides* and *Centropages*. Clearance rates decreased exponentially with increased prey concentration.

CHAPTER 4

SMALL JUVENILE HORSE MACKEREL: FEEDING BEHAVIOUR, SELECTIVITY AND CLEARANCE RATES.

This chapter is very similar to the previous except that it describes the results from eight experiments performed on small juveniles ca. 80-100 mm long (Table 4.1). The aims and methods used are the same as for large juveniles so that a comparison of feeding behaviour of these two fish sizes can be made. Detailed results are from two experiments in which food consisted of mixed copepods of a wide size range (Expt. 7) and large prey of a single type (Expt. 1), respectively.

4.1: Feeding behaviour.

The small juvenile horse mackerel fed in the same manner as large juvenile horse mackerel. Fish size appeared not to have any effect on the methods they apply when feeding.

Expt 7: mixed copepods

The average swimming speed when not feeding was 0.46 ± 0.09 (SD) body length per second ($BL.s.^{-1}$). After addition of food into the tank, the fish became excited and broke their shoals, increased their swimming speeds and started feeding immediately. Average swimming speed increased almost 4–fold compared to non-feeding fish, to a level of 1.80 ± 0.56 $BL.s.^{-1}$ but when the food was depleted swimming speeds decreased and returned to non-feeding levels (Fig. 4.1).

Table 4.1. Small juvenile horse mackerel: summary of the experiments, showing the number of fish, starvation period, fish size, duration of each experiment, prey type and size and water temperature for each feeding experiment performed.

Experiment number	No. of fish	Starvation time (days)	Fish size, (TL, ±SD, mm)	Duration (minutes)	Prey type	Prey size (µm)	Temp (^{0}C)
Small juveniles							
1	30	2	89.4 ± 8.4	75	Mysids	9729.0 ± 1038.3	18.0
2	34	2	89.4 ± 5.7	75	Mysids	9187.3 ± 1564.7	16.5
3	34	2	89.5 ± 8.6	60	Mysids	9364.7 ± 1528.6	15.6
4	34	3	89.5 ± 7.6	60	Mysids	11338.7± 1062.5	19.0
5	34	1	90.2 ± 9.2	60	Mixed copepods	1052. ± 538.9	16.5
6	32	2	90.5 ± 10.7	60	Mixed copepods	601.7 ± 273.8	17.0
7	32	1	90.6 ± 7.8	60	Mixed copepods	1579.7 ± 1023.3	16.0
8	30	2	90.6 ± 7.2	60	Mixed copepods	716.7 ± 274.6	14.5

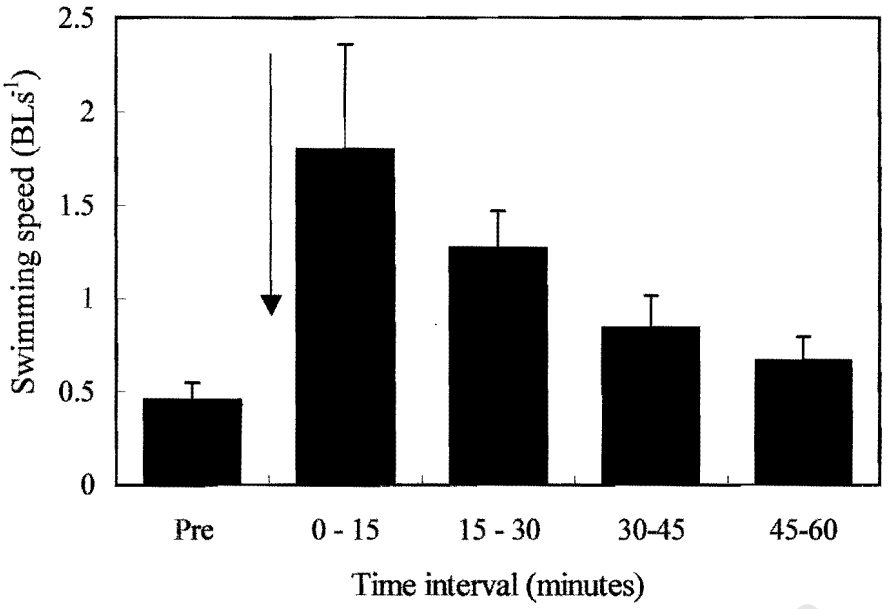

Fig. 4.1. Small juvenile horse mackerel: mean swimming speeds (+ 1SD) at different time intervals before and after food was introduced into the tank, Expt. 7. The arrow shows when food was introduced.

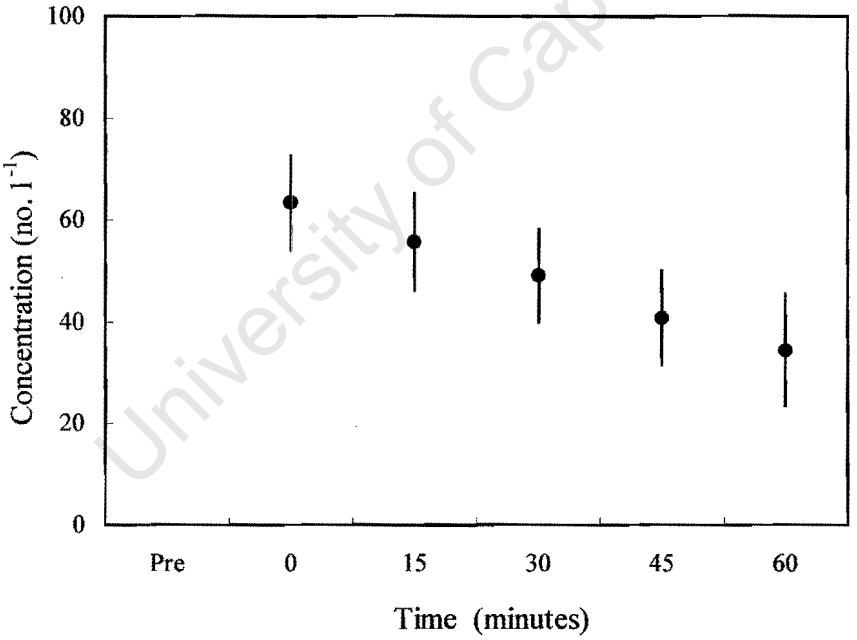

Fig. 4.2. Small juvenile horse mackerel: decrease in prey concentration (mean ± 2SD) as a function of time after food was introduced into the tank during Expt. 7.

Food concentration was observed to decrease with time (Fig. 4.2). Prey items used in Expt. 7 (Fig. 4.3) consisted of a variety of crustacean zooplankton ranging from 0.2 to 2.0 mm, *Oithona* (26%), *Acartia* (21%), the 'other' group (19%) (*Calanus*, *Centropages*, *Oncaea*, harpacticoids and copepod nauplii), small copepods (18%), and cirripede nauplii (10%) were the major prey categories at the start of the experiment. By the end of the experiment (t=60) there had been a slight change in the species composition, i.e. species in the 'other' group had shown a slight decrease from 19 – 12% and *Oithona* spp. had increased from 26 - 35% (Fig. 4.3). Prey size frequency distributions at each sampling interval show that large particles (1.6-2.0 mm) were preferentially removed, with small particles (0.2–1.4mm) remaining at the end of the experiment (Fig. 4.3).

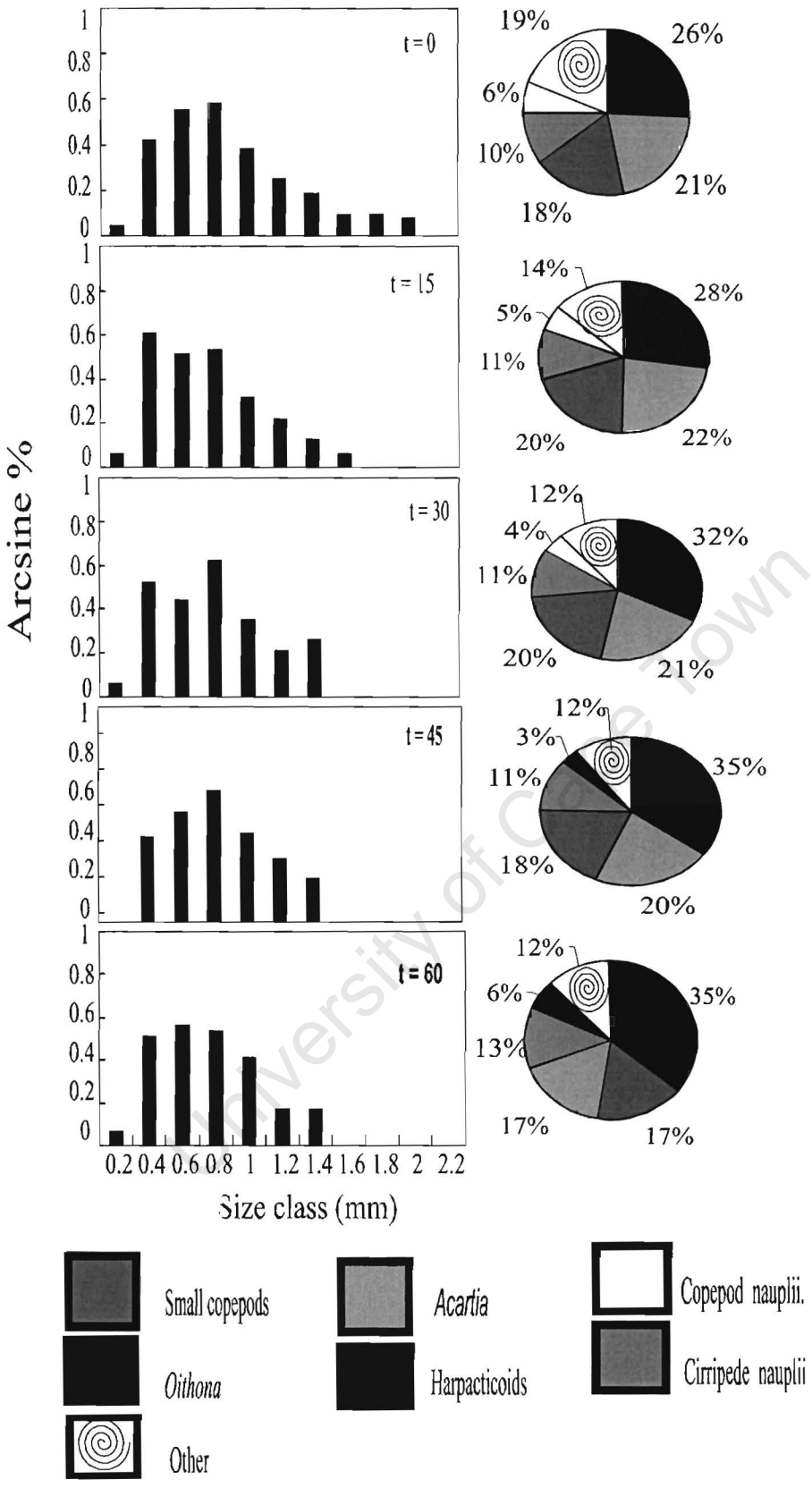

Fig. 4.3. Small juvenile horse mackerel: size frequency distribution and prey composition of prey used in Expt. 7 as a function of time after food was introduced into the tanks.

Concentrations of the major prey types at each sampling time during Expt. 7 are shown in Fig. 4.4. Initial concentrations of large calanoid species (*Calanus* and *Calanoides*) were very low, and both species had almost totally disappeared at t = 15. Concentrations of *Calanus* (one – way ANOVA, $F = 36.13$, $df = 4, 45$, $p < 0.0001$) and *Calanoides* (one – way ANOVA, $F = 42.50$, $df = 4, 45$, $p < 0.0001$) decreased significantly between successive time intervals. *Centropages* and *Acartia* were both found at all time intervals, although *Centropages* were very sparse whilst *Acartia* were abundant in all samples. As time proceeded mean concentrations of both *Acartia* (one – way ANOVA, $F = 31.15$, $df = 4, 45$, $p < 0.0001$) and *Centropages* (one – way ANOVA, $F = 37.20$, $df = 4, 45$, $p < 0.0001$) also decreased significantly.

Very few of the small zooplankton showed a rapid change in concentration (Fig. 4.4) when compared with the large calanoid copepods, although small copepods showed a marked decrease towards the end of the experiment (Fig. 4.4). The concentrations of small copepods were significantly different between successive time intervals (one – way ANOVA, $F = 41.55$, $df = 4, 45$, $p < 0.001$). Groups such as harpacticoids and *Oncaea* spp. also showed a decline in their concentrations, although the reduction in their concentrations was not as fast as those of species already mentioned. Concentrations were significantly different with time for harpacticoids (one – way ANOVA, $F = 19.53$, $df = 4, 45$, $p < 0.05$), *Oncaea* spp. (one – way ANOVA, $F = 23.82$, $df = 4, 45$, $p < 0.05$), *Oithona* spp. (one – way ANOVA, $F = 11.97$ $df = 4, 45$, $p < 0.05$),

and copepod nauplii (one – way ANOVA, $F = 22.47$, $df = 4, 45$, $p < 0.05$) except for the concentration of cirripede nauplii which did not differ significantly (one – way ANOVA, $F = 3.29$, $df = 4, 45$, $p > 0.05$).

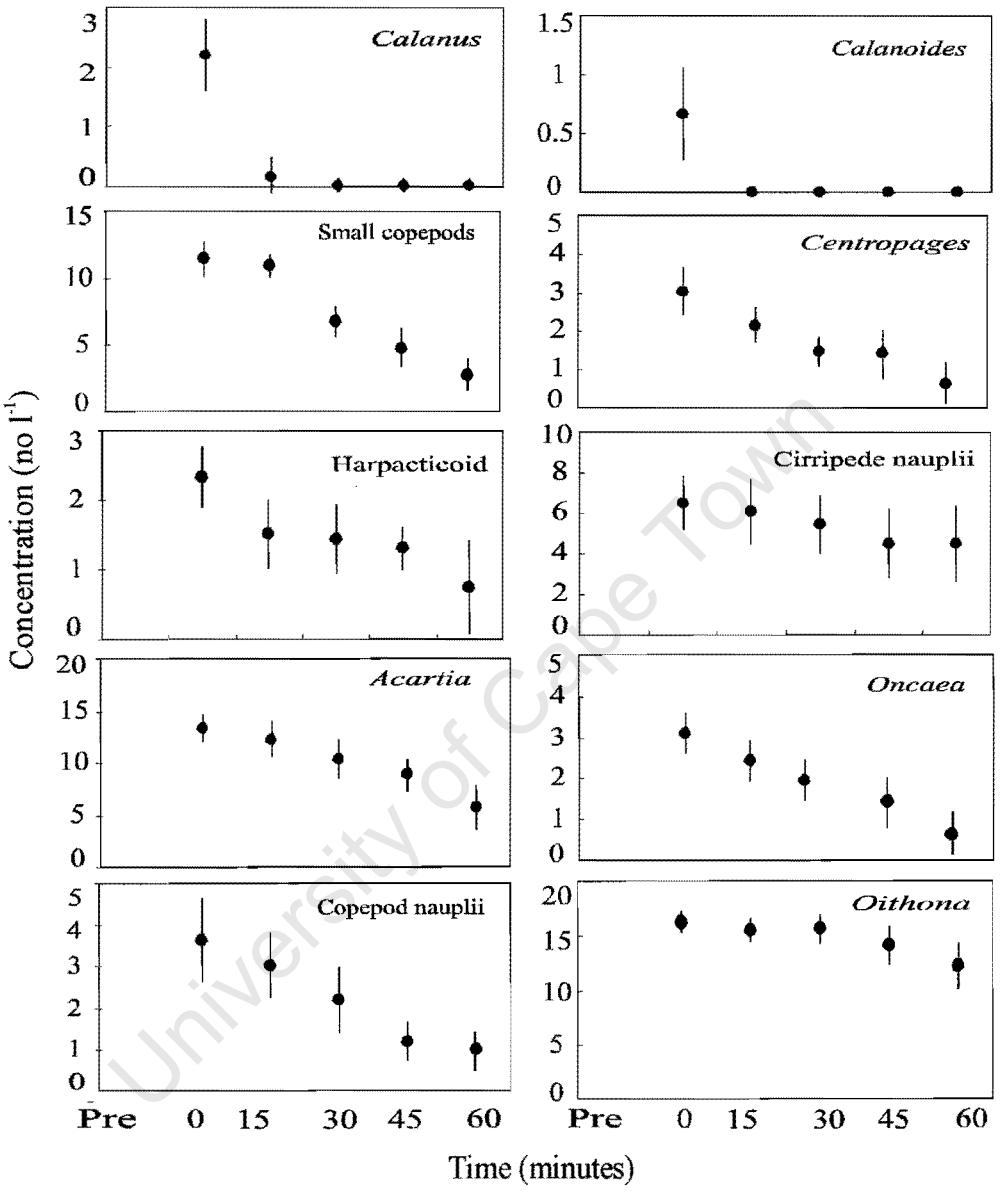

Fig. 4.4. Small juvenile horse mackerel: influence of prey type concentrations (mean ± 2SD) as a function of time after introduction of food into the tank during Expt. 7.

Changes in the concentration of prey size classes at each sampling interval are shown in Fig. 4.5. This shows that large prey items >1.0 mm were removed faster than smaller ones (<1.0 mm) also changes in the concentrations of all size classes (Table 4.2) among time intervals were significant (one – way ANOVA, $p < 0.05$).

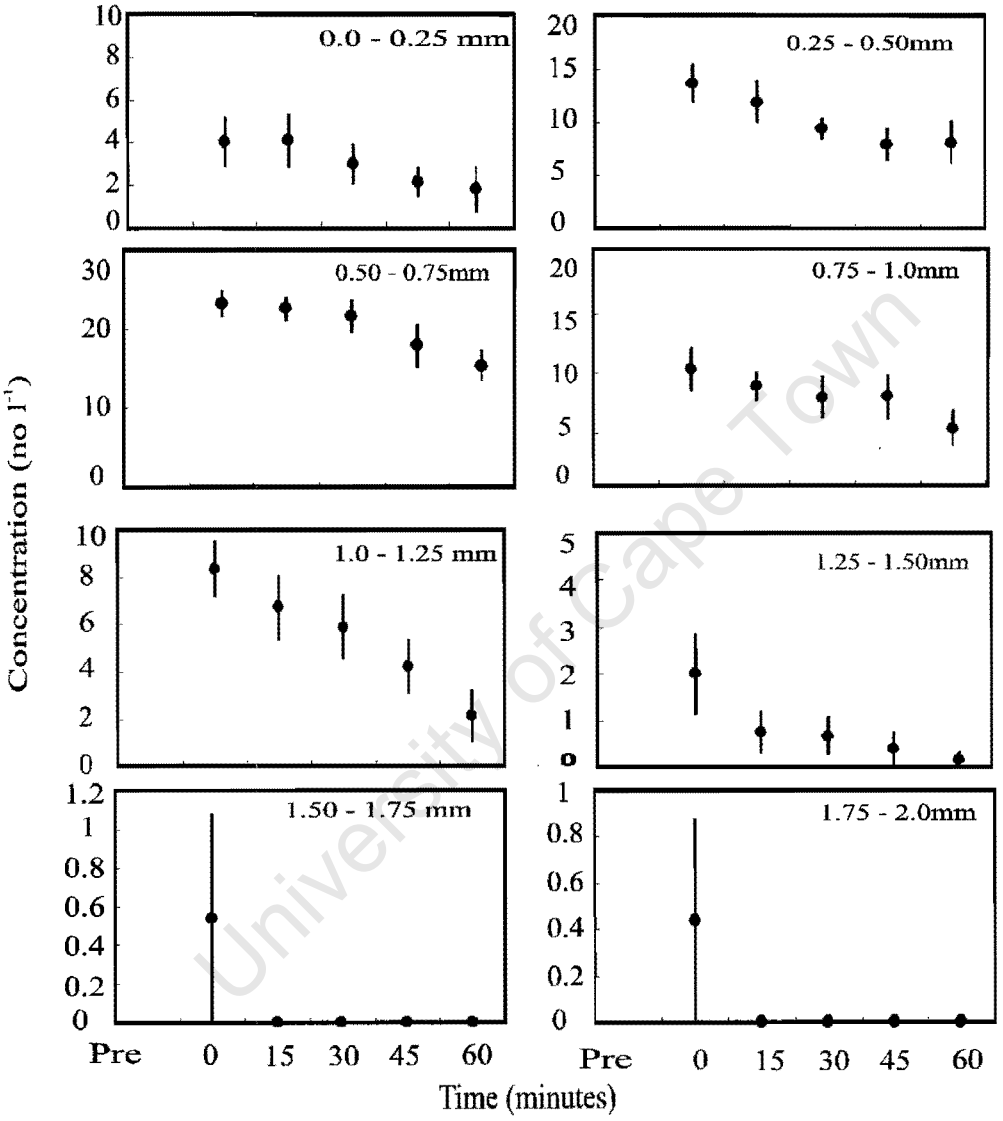

Fig. 4.5. Small juvenile horse mackerel: influence of size on prey concentrations (mean ± 2SD) as function of time after introduction of food into the tank (Expt. 7).

Table 4.2. Feeding of small juvenile horse mackerel: One – way ANOVA of concentrations (no. l^{-1}) of different size classes of mixed .

Size class (mm)	F values	df	p-value
0.0-0.25	8.43	4, 45	<0.01
0.25-0.50	26.14	4, 45	<0.001
0.50-0.75	33.48	4, 45	<0.001
0.75-1.0	14.58	4, 45	<0.01
1.0-1.25	41.91	4, 45	<0.001
1.25-1.50	30.63	4, 45	<0.001
1.50-1.75	48.30	4, 45	<0.001
1.75-2.0	42.54	4, 45	<0.001

Large prey, with large carbon contents, were mostly preferred consumed by small juvenile horse mackerel when compared to the smaller prey. Fig. 4.6 shows the same pattern as Fig. 4.3 in which large copepods were removed faster than small ones.

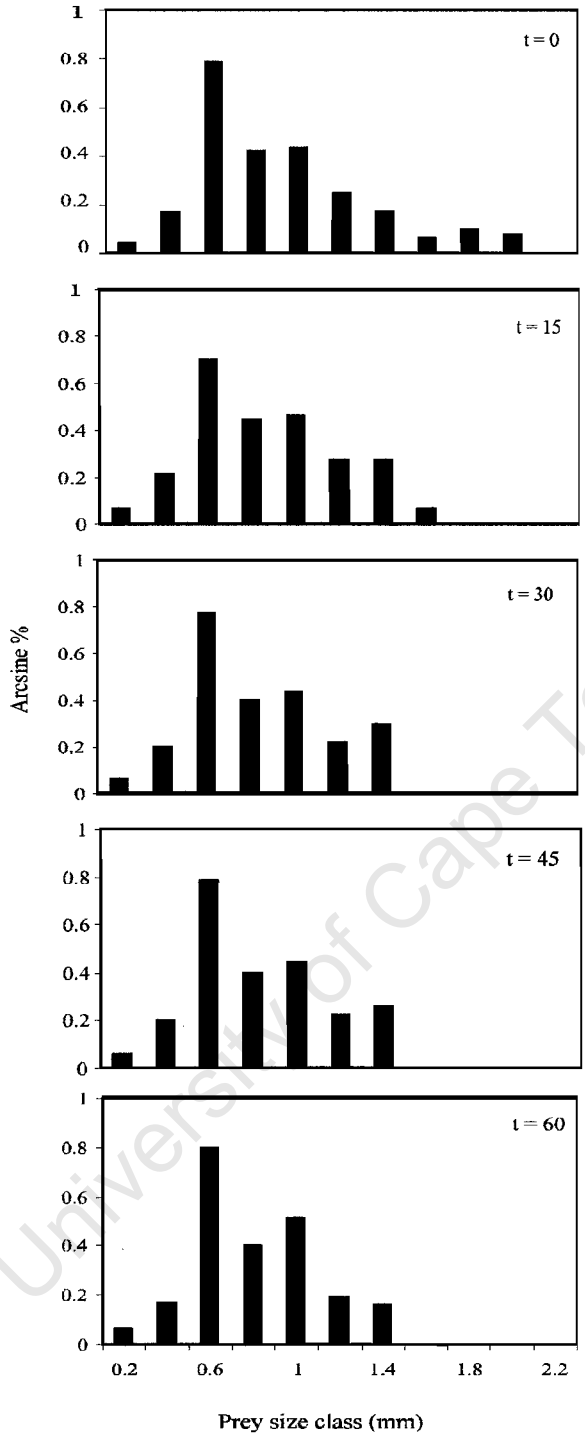

Fig. 4.6. Small juvenile horse mackerel: frequency distribution of carbon content (mg l^{-1}) by size, remaining in the tank at successive time intervals during Expt. 7, using mixed copepods.

4.1.2 Expt. 1: Mysids

Results obtained from Expt. 1 in which a single large prey type, (mysids) was used, showed that small juvenile horse mackerel responded in the same manner as in Fig. 4.1, increasing the swimming speed at the beginning of the experiment from an average of 0.68 ± 0.07 $BL.s^{-1}$ to 1.71 ± 0.18 $BL.s^{-1}$ when feeding and later decreased with decreasing prey concentration closer to the level of non-feeding (Fig. 4.7). Size frequency distributions throughout the experiment indicate that the proportion of small size classes decreased with time. This is confirmed by the results from a one – way ANOVA (Table 4.3) conducted for each size class, the concentration of small size classes decreased with time, particularly the smallest size (Fig. 4.8) whereas the size class 9.0-10.5mm showed no significant change ($p > 0.05$) in concentration (Fig. 4.9), and 13.5 mm size class was only encountered at $t = 0$ only.

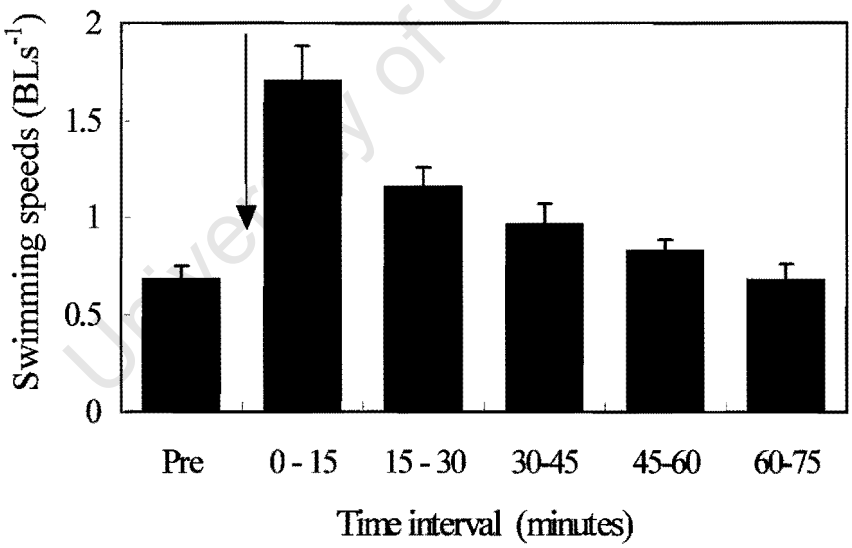

Fig. 4.7. Small juvenile horse mackerel: mean swimming speeds (+ 1SD) at different time intervals before and after food was introduced into the tank, Expt. 1. The arrow shows when food was introduced.

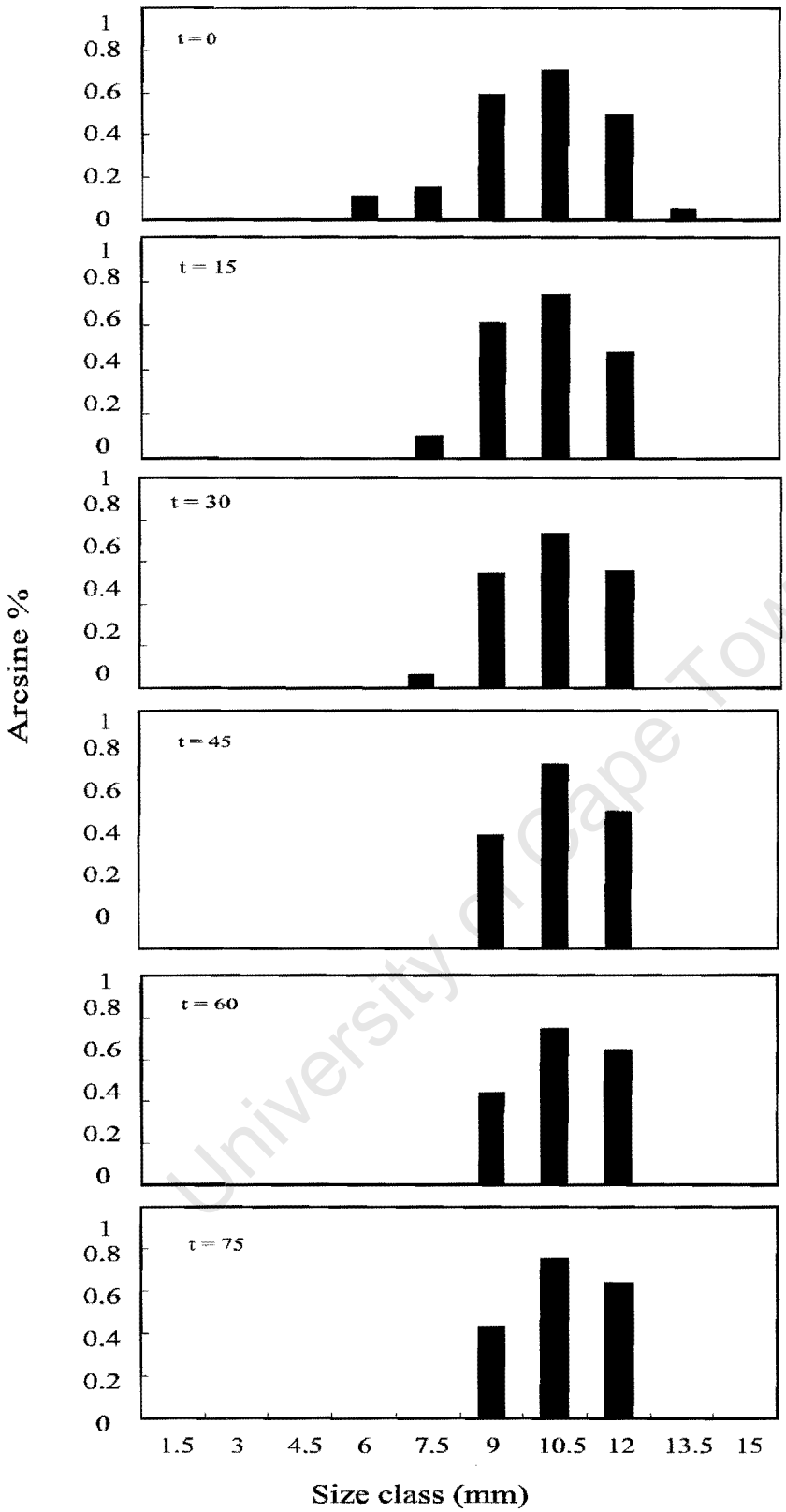

Fig. 4.8. Small juvenile horse mackerel: size frequency distribution of mysids at successive time intervals after introduction of food to the tank during Expt. 1.

Table 4.3. Feeding of small juvenile horse mackerel: One –way ANOVA of concentrations (no. l^{-1}) of different size classes of mysids.

Size class (mm)	F values	df	p-value
4.5 - 6.0	16.8	5, 54	<0.0005
6.0 - 7.5	24.32	5, 54	<0.0005
7.5 - 9.0	24.37	5, 54	<0.0005
9.0 - 10.5	3.90	5, 54	>0.05

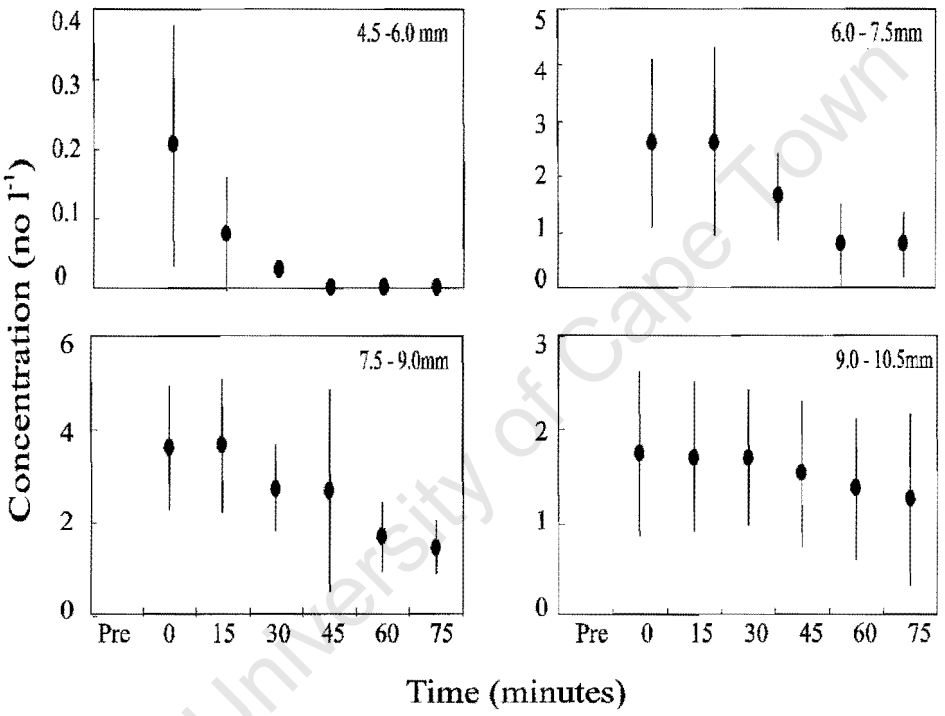

Fig. 4.9. Small juvenile horse mackerel: mean concentration (± 2SD) for mysid size classes as a function of time (minutes), Expt. 1.

Large mysids contributed a large proportion of carbon to the food environment and small juveniles appeared to remove mostly the smallest mysids although the largest mysids (13.5 mm) were removed first (Fig. 4.10).

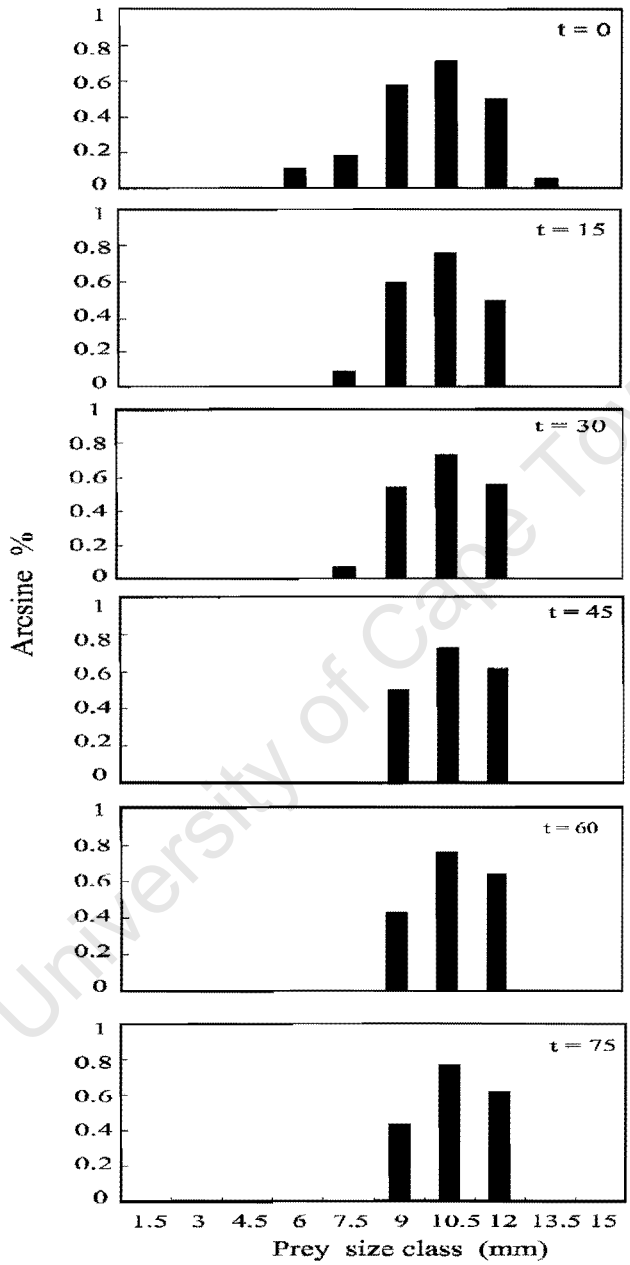

Fig. 4.10. Small juvenile horse mackerel: size frequency distribution of carbon content (mg l^{-1}) by size of prey (mysids) at different time intervals after food was introduced into the tank during Expt. 1.

4.2. Combined results: effect of prey size and/or concentration on fish swimming speed.

Both prey size (Fig. 4.11A) and prey concentration (Fig. 4.11 B) had no influence on the rate at which the fish swim, and significant relationships between swimming speed and either prey size or concentration could not be derived.

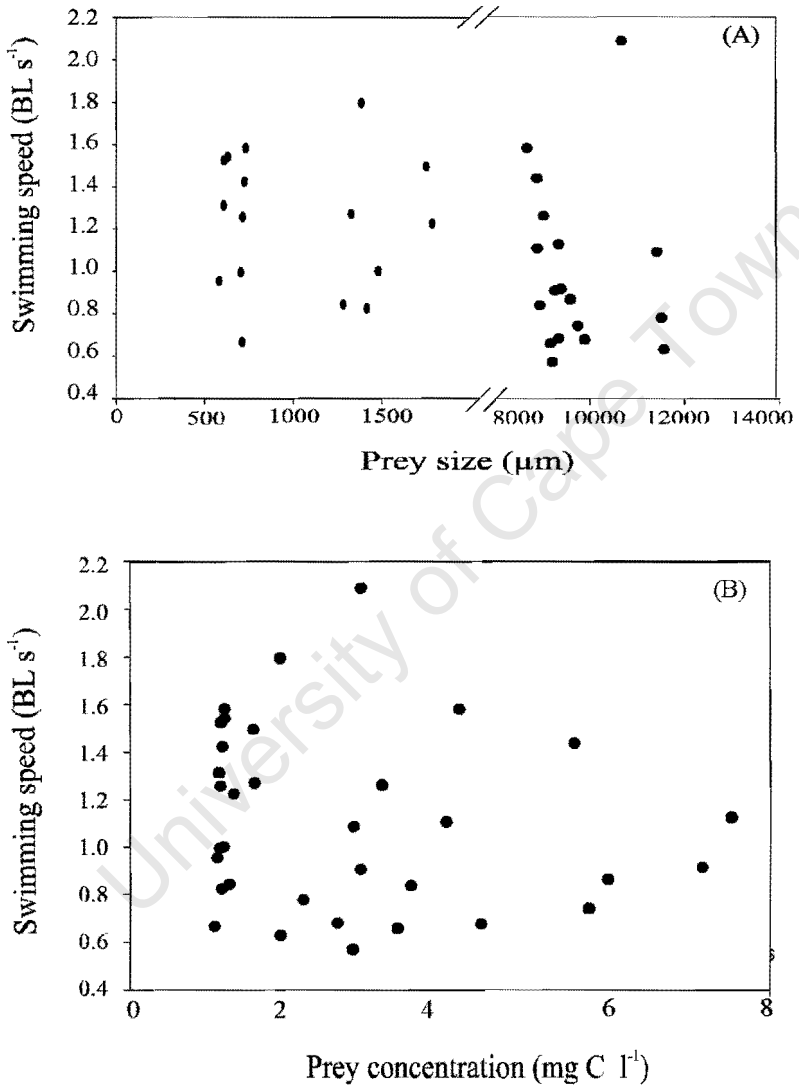

Fig. 4.11. Small juvenile horse mackerel: effect of (A) prey size and (B) concentration on the swimming speed of horse mackerel.

4.3. Clearance rates

Combining clearance rates for all experiments conducted on small juvenile horse mackerel showed that clearance rates varied with prey size (Fig. 4.12). Large food particles ranging from 7.50 – 10.50 mm were removed at very slow rates between 0.43 – 2.43 l $fish^{-1}$ $min.^{-1}$, whereas those smaller in size (ranging from 1.25. to 3.0 mm) were cleared faster at a rate from 1.01 to 6.0 l $fish^{-1}$ $min.^{-1}$. The remaining prey < 1.25 mm had very slow clearance rates similar to those of large prey. The relationship between clearance rate (F) and prey size (x) was described using a quadratic regression equation, which showed that clearance rates increased with increasing particle size for prey of up to 3.0 mm TL, but clearance rate decreased for very large particles:

$$F = 0.14 + 1.86 * x - 0.178 * x^2 \text{, } r^2 = 0.36, n = 36, p < 0.001 \quad \text{.....(4.1)}$$

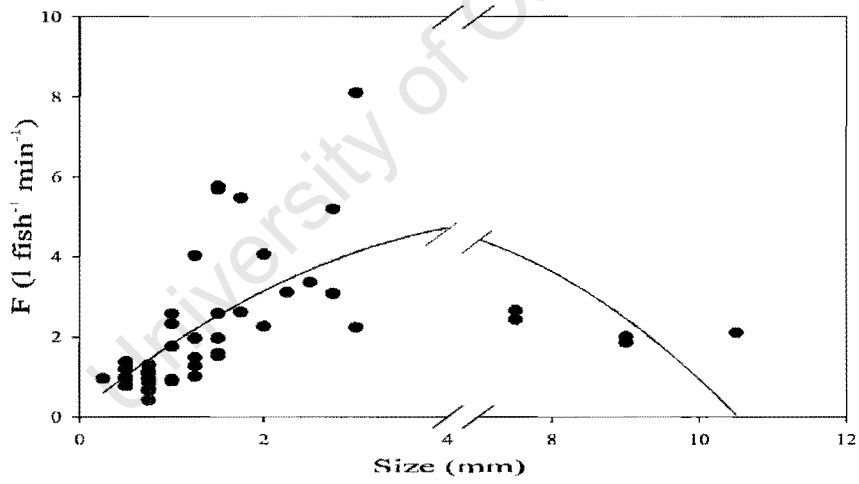

Fig. 4.12. Small juvenile horse mackerel: clearance rate (F) as a function of prey size-class obtained from all the feeding experiments.

Clearance rates were also examined as a function of time within an experiment. Fig. 4.13A indicates that at the beginning of the experiment (i.e. between 0 - 15 minutes) fish were feeding at similar rates on most of the prey organisms available. After the first 15 minutes, fish started to select particular prey types, showing faster clearance rates on large prey. For example, clearance rates for prey such as *Calanus* increased after the first 15 minutes from about 2.0 to 5.0 l fish^{-1} min.$^{-1}$, compared to 0.70 – 1.90 l fish^{-1} min.$^{-1}$ for small prey such as *Oithona* and small copepods. Clearance rates were also affected by prey concentration (number per litre) during an experiment, decreasing with increasing prey concentration (Fig. 4.13 B). The relationship is described by an exponential decay curve:

$$F = 5.18\ e^{0.09conc} \qquad (r^2 = 0.42, p < 0.05), \qquad \text{.....(4.4)}$$

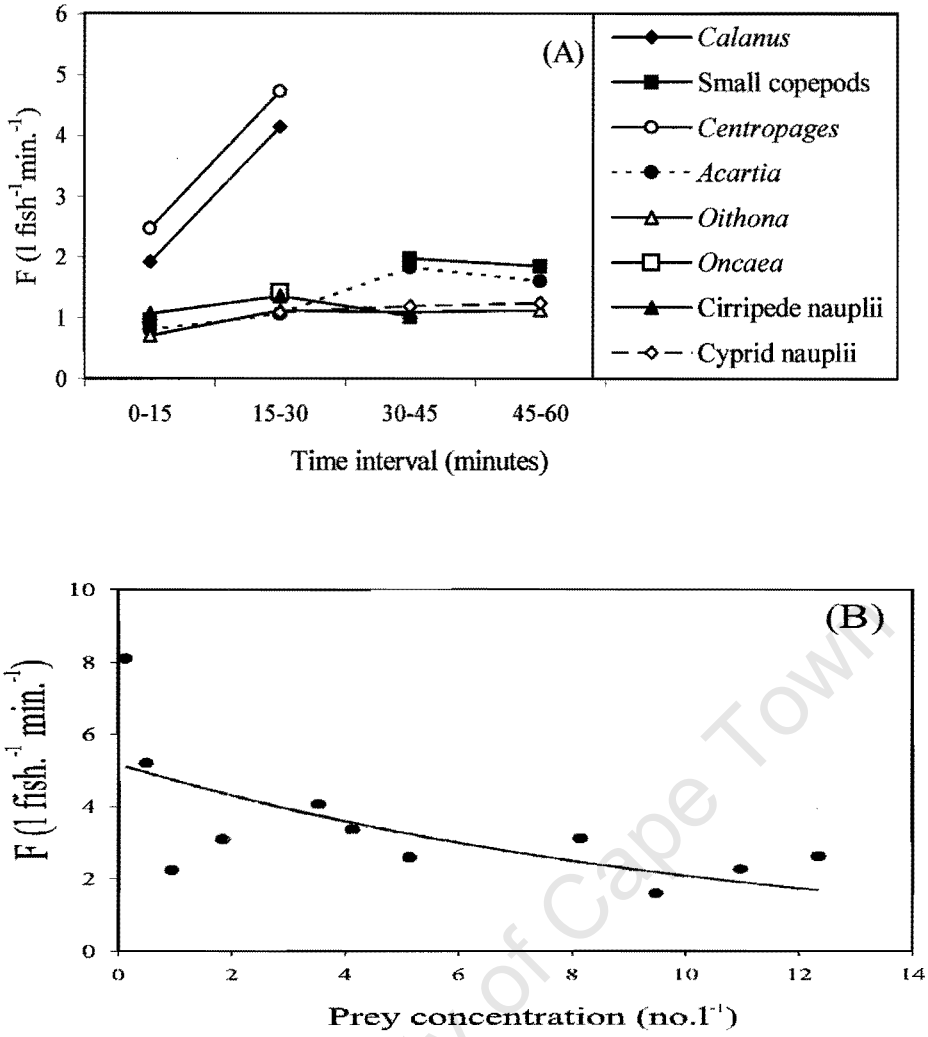

Fig. 4.13. Small juvenile horse mackerel: A) Clearance rate (F) as a function of time interval, and (B) as a function of prey concentration in Expt. 1.

In summary, small juvenile horse mackerel exhibit size selectivity, especially when offered mixed zooplankton. The relationship between clearance rate and prey size was dome – shaped, with slow clearance rates on very large prey particles. This reduction in clearance rates at large prey sizes is presumably due to difficulty in handling large prey. Clearance rate increased to a maximum after 15-30 minutes for *Calanus* and *Centropages*, but remained low for other prey types. Clearance rates declined exponentially with prey concentration.

CHAPTER 5

DISCUSSION AND CONCLUSIONS

5.1: Feeding behaviour

This work confirms experimentally that horse mackerel capture prey over a wide range of size classes using particulate feeding only. Like many other particulate feeders, juvenile horse mackerel capture their prey with their protrusible mouths (Lazarro 1987) that are well adapted for sucking prey items into their buccal cavities with water. In contrast, sardine and anchovy in the southern Benguela system exhibit two feeding modes, filter and particulate feeding, depending on the size and concentration of food available (van der Lingen 1994).

The mouths of sardine and anchovy are slightly protrusible, but not to the same extent as juvenile horse mackerel. When filter feeding, these clupeid species capture their prey by keeping the mouth agape while swimming, and retaining the prey on entrapment structures such as gill arches (Lazzaro 1987). The difference between the two feeding modes is that particulate feeding fish can visually detect and select individual prey. In contrast, filter feeders do not visually detect and target individual items but strain food particles from the surrounding water (Lazzaro 1987).

Horse mackerel, like many fish, behave differently when feeding and when not. In the absence of food, they kept in tight schools, swam slowly, occasionally stopping and then continuing, all in the same direction (Chapters 3 and 4). Once food was added to the tank, fish started feeding immediately, increased their swimming speeds, stopped schooling and swam in different directions, each fish pursuing its prey. Similar findings were reported by Gibson and Ezzi (1985), when in the absence of food, herring *Clupea harengus* circled around the tank swimming in tight shoals. When food was added they broke their shoals. The loose aggregation of planktivorous fish during particulate feeding is advantageous because it decreases the overlap of the visual fields of the fish and allows the fish to feed effectively upon the available prey (James and Findlay 1989). If fish remain in a tight school when feeding, the potential volume searched would be reduced (Eggers 1976).

5.1.1: Feeding selectivity

The present findings show that large juvenile horse mackerel are selective feeders preferentially selecting large particles although small juveniles cannot capture large prey effectively. Initially when small and large juvenile horse mackerel were offered mixed copepods, prey particles were distributed between 0.2–2.8 mm (Chapter 3) and 0.2–2.0 mm (Chapter 4), but at the end of each experiment (t=60) the remaining particle sizes ranged between 0.2–1.4 mm. Results indicate that once large prey had been consumed, juvenile horse mackerel switched to feed on smaller prey. Similar trends were found in

laboratory studies done by Werner and Hall (1974) for juvenile bluegill sunfish *Lepomis machrochirus* feeding upon different sizes of cladocerans *Daphnia magna.* They demonstrated that prey preference is proportional to size, with bluegills starting to feed on the small cladocerans only after the abundance of large prey had decreased.

Large food particles (e.g. calanoid copepods) contribute more carbon to horse mackerel diet than smaller crustaceans. They probably feed initially on large zooplankton to maximise energy gain per feeding event. Whereas sardine and anchovy derive their carbon both from phytoplankton and zooplankton, zooplankton contributing greater amounts than the phytoplankton for both species (van der Lingen 2002), horse mackerel obtain their carbon from zooplankton only. Both sardine and anchovy benefit from zooplankton as their dominant food source although they consume different components of the zooplankton and they appear to partition this resource on the basis of size (van der Lingen 1994).

Small copepods (<1.2 mm), cyclopoid copepods, crustacean eggs and nauplii contribute most to the dietary carbon of sardine. The small quantity of large food particles (>1.2 mm) found in the stomachs of sardine indicates relatively little particulate feeding (van der Lingen 1994). In contrast, anchovy derive most of their carbon from large (>1.0 mm) zooplankton, e.g. calanoid copepods and euphausiids, captured through size-selective particulate feeding, but they can also filter-feed (James 1987). Because of their size

selective feeding behaviour it is probable that horse mackerel, like anchovy, also derive their carbon from large zooplankton (calanoid copepods and mysids), using particulate feeding only. In this study, mysids were used and the response to the food type differed according to size. Large juveniles selected prey > 6.0 mm and prey concentrations decreased irrespective of size, whereas small juveniles selected small mysids in preference to larger ones.

Availability of prey appeared to have an influence on the feeding behaviour of horse mackerel (Figs. 3.1, 3.7, 4.1 and 4.7). Introduction of food into the tank influenced swimming speed of both large and small juveniles which later decreased with time as prey abundance decreased and as fish continued to feed (Figs 3.2 and 4.2). Swimming speeds of large juvenile horse mackerel were also influenced by the prey size and concentration, with large prey particles (Fig. 3.13A) and high prey carbon concentrations (Fig. 3.13B) inducing fast swimming and resulting in increased energy being used to capture the prey, while small juvenile horse mackerel were not affected by either prey size or concentration. Fish select large prey when feeding to re-gain the energy lost while foraging. As prey size and concentrations decrease, horse mackerel reduce their swimming speeds so as to reduce the loss of energy. Gerking (1994) describes this as a cost: benefit analysis in energetic terms.

5.1.2: Clearance rates

Clearance rates varied with particle size for different size groups of juvenile horse mackerel. When fed mixed copepods, clearance rates increased with increasing prey size for large juveniles, an asymptotic maximum value of 10.23 l fish.$^{-1}$ min.$^{-1}$ being attained for prey of 0.50-2.0 mm (Fig. 3.12). There is a steep increase in clearance rate at prey sizes between 0.5 and 2.0mm, giving a marked sigmoid curve. In small juveniles, clearance rates increased at first with increasing size and later decreased with very large prey (Fig. 4.12), reaching a maximum clearance rate (~5.0 l fish.$^{-1}$ min.$^{-1}$) of about half that of large juveniles (10 l fish.$^{-1}$ min.$^{-1}$). This reduction is likely due to gape size making it difficult for the fish to handle large prey. Prey may require manipulation before they can be swallowed, e.g. reduced to the size that can be swallowed by a fish (Helfman 1994). Because of their smaller gape size, small fish would initially select small zooplankton. The smallest and the least evasive species of zooplankton are preferentially selected first (Lazzaro 1987), as was found for small mysids with the small juveniles under study.

Mysids have a strong escape response when attacked and they also tended to sink to the bottom after they were added to the tank, or stick to the walls of the tanks, making them inaccessible to the fish. The inability of fish to ingest large zooplankton has been observed in Alewife *Alosa pseudoharengus* and Ciscoes *Coregonus hoyi* and *C. artedii.* When fed mysids, amphipods and calanoid copepods, these fish could not handle large

prey because of their small mouth size (Janssen 1978). Zaret (1980) reported that planktivorous fish are gape-limited predators with mouth diameter or gape limiting the maximum size of prey they can swallow. However, visual acuity can also affect feeding behaviour, food organisms are perceived at short distances, and are often difficult to capture because of poor perception of the prey, a result of inexperience of young fish (Lazzaro 1987).

Food clearance rate was inversely proportional to prey concentration. When viewed as a function of time, clearance rates increased for all prey species. Regarding a predator's characteristics, satiation is believed to be an important feature that affects the feeding behaviour of fish (Durbin *et al* 1981). In this study, there was some evidence of satiation, when swimming speeds decreased (Figs 3.1 and 4.1) during the experiments as prey concentration and hunger decreased with time. Ware (1972) showed that pursuit rate in fish decreases with decreasing hunger and the handling time of prey increases when approaching satiation.

The present experiments were designed to determine the clearance rates as a function of size, but other parameters such as prey type appeared to have an influence on the rate at which the prey particles were cleared. For example, when large juveniles were offered mixed prey assemblages, clearance rates as a function of prey type (plotted as mean size of that prey type) indicated that calanoid copepods (*Calanus, Calanoides* and

Centropages) were cleared faster than the small copepods. Small prey such as small copepods, and *Oithona* were cleared very slowly although other small prey, e.g. *Oncaea,* induced fast clearance rates. Hence, prey size is not the only factor influencing clearance rates, and the results obtained for *Oncaea* spp. suggest that this species may be more easily perceived than other zooplankton. Large prey species like mysids, which would be expected to be cleared fast due to their size, had slower rates than expected. This may be attributed to their ability to escape capture since mysids are strong swimmers (Fig. 5.1).

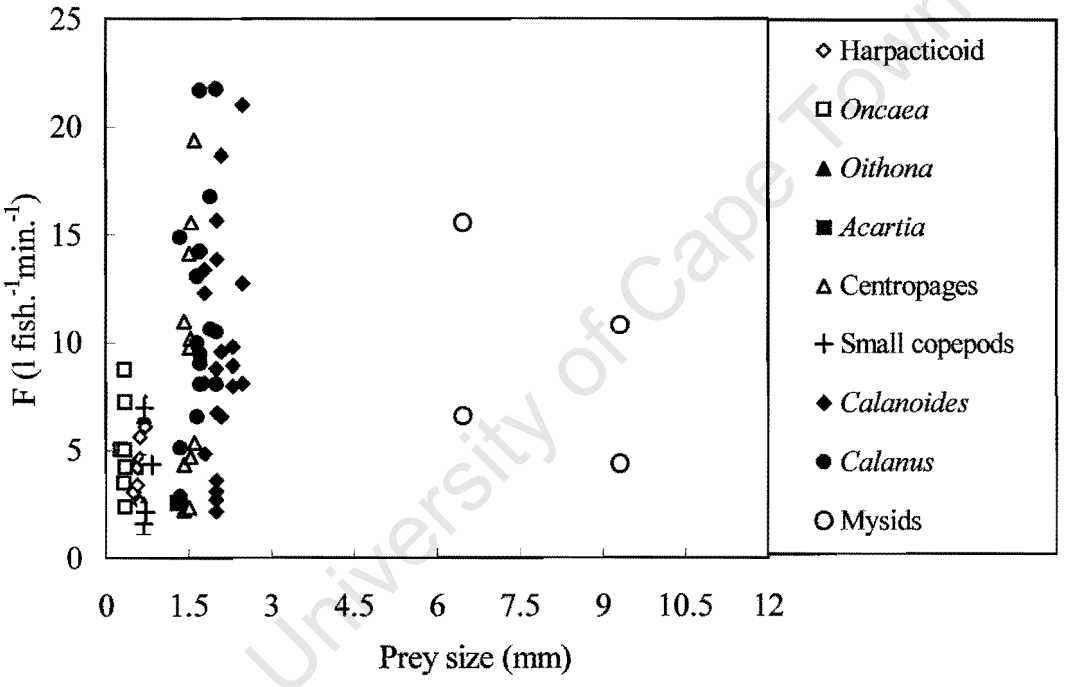

Fig. 5.1. Large juvenile horse mackerel: Clearance rate (F) as a function of prey type (size) all experiments combined.

Small juveniles also cleared large calanoid copepods (*Calanus, Calanoides,* and *Centropages*) faster than small prey, and *Oncaea* spp. again appeared to be an exception.

Large prey like mysids cleared slowly when compared to some small prey (Fig. 5.2), attributed to prey handling problems as discussed above.

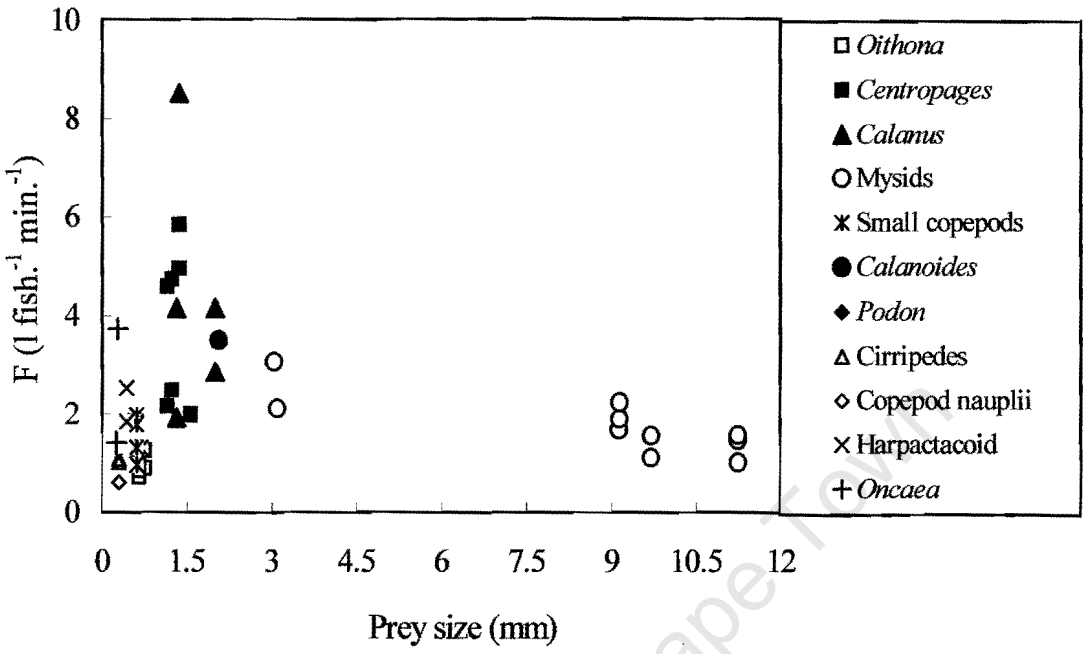

Fig. 5.2. Small juvenile horse mackerel: Clearance rate (F) as a function of prey type, all experiments combined.

Oncaea were cleared at fast rates by both small and large juveniles, despite their small size, which might be due to their visibility because they would appear darker than their background. Supportive evidence is given by Arthur (1976) who found that jack mackerel *Trachurus symmetricus* larvae preferentially selected brightly coloured organisms such as harpacticoid copepods *Microsetella norvegica*. Apart from their size, calanoid copepods also possess other features that may make them more visible to predators, e.g. appearance, motion and shape.

The motion of prey also attracts the attention of the predator. Ware (1973), found that moving prey were more successfully detected by rainbow trout *Salmo gaidneri*, than non-moving prey. Copepods (calanoids and cyclopoids) are believed to be able to accelerate rapidly using their four ventrally situated pairs of legs for powerstrokes, and can sustain great speeds and manoeuvre quickly due to their flexible bodies and their movable appendages, which can all be used for locomotion. Once copepods are within the visible range of a fish, motion may increase their conspicuousness (Lazzaro 1987). Therefore, in a mixed prey species assemblage, it may not always be the largest species that are selected by the planktivores, but also prey with other characteristics that make them more visible.

The present results suggest that cyclopoids were selected only when calanoids were depleted. Lazzaro (1987) postulated that within the visible range of the fishes' vision, motion increases the conspicuousness of a prey. Utne – Palm (2000) also concluded that prey body movement should be considered as one of the primary model inputs in explaining prey selection.

5.2: Estimation of time to attain daily ration

The clearance rate values reported in this study may be used in conjunction with average biomass estimates of zooplankton in the southern Benguela region to estimate

consumption rates and hence the time required to attain daily ration for horse mackerel juveniles. Pillar and Barange (1998) estimated horse mackerel daily ration in the southern Benguela at 3.8 % wet body mass per day (WBM d^{-1}). In this study, the times required to attain daily rations between 2 and 6 % WBM d^{-1} were estimated in order to assess whether the experimental results reported here are ecologically meaningful

To estimate the time required to obtain daily ration, zooplankton were divided into two classes: small zooplankton of < 1.75 mm and large zooplankton of > 1.75 mm. This division was chosen on the basis of large juvenile feeding behaviour (see Fig. 3.12), where clearance rate is different below and above this prey size. For small zooplankton, prey size was set at 0.875mm TL and for large zooplankton was set at 2.325mm TL. Clearance rates for both large and small juvenile horse mackerel feeding on both prey sizes were calculated using equations 3.3 and 4.3 respectively. The clearance rate values obtained were:

$$F_{LL} = 10.23 \text{ l fish.}^{-1}\text{min.}^{-1}$$

$$F_{LS} = 3.18 \text{ l fish.}^{-1}\text{min.}^{-1}$$

$$F_{SL} = 3.55 \text{ l fish.}^{-1}\text{min.}^{-1}$$

$$F_{SS} = 1.63 \text{ l fish.}^{-1}\text{min.}^{-1}$$

where F_{LL} is the clearance of large juvenile horse mackerel feeding on large zooplankton, F_{LS} is for large juvenile horse mackerel feeding on small zooplankton, F_{SL} is for small juvenile horse mackerel feeding on large zooplankton, F_{SS} for small juvenile horse mackerel feeding on small zooplankton.

The clearance rates were used together with the estimated zooplankton biomass to derive consumption rates. Estimates of zooplankton biomass were obtained from various authors, i.e. for mesozooplankton (large zooplankton) estimates were provided by Andrews and Hutchings (1980), Pillar (1984a, 1984b), Hutchings (1985), Peterson *et al* (1990), Verheye (1991). For microzooplankton (small zooplankton) the estimates were reported by Verheye *et al* (1992) and Hutchings *et al* (1995). These depth- integrated zooplankton estimates were reported as underestimated, since they assume vertical distribution to be homogeneous, and the reports on depth-stratified sampling had shown that this is seldom the case (Verheye and Hutchings, 1988 and Verheye *et al*, 1992).

Also most of the data on zooplankton abundance in the Benguela system has been derived from nets with a mean size of 200 µm or greater (Verheye *et al* 1992) and these nets have been shown to underestimate the small zooplankton biomass (Painting *et al* 1993), retaining within the total zooplankton only the copepods with body width that is larger than the mesh width (Pillar 1984a).

Based on the above-mentioned reasons, the published zooplankton densities in the southern Benguela ecosystem are considered to be underestimated. Therefore, constant estimates of 0.2 mg C. l^{-1} were used for small and 0.05 mg C. l^{-1} for large zooplankton (Verheye and Hutchings, 1988, and van der Lingen, 1999).

Wet mass = 10 x dry mass (H. M. Verheye, MCM, pers. comm.)

Carbon = 0.424 x dry mass (van der Lingen 1999)

Small zooplankton carbon concentration:

C_s= 0.2 mg C l^{-1} (Verheye and Hutchings 1988)

= 0.2 x 2.3585 mg DM l^{-1} (= 1/0.424 = 2.3585mg DM. mgC^{-1}) (Table 2.2)

= 0.472 mg dry mass l^{-1}

= 0.472 x 10 = 4.72 mg wet mass l^{-1} (H. M. Verheye, pers. comm.)

For large zooplankton:

C_L = 0.05 mg C. l^{-1} (Verheye and Hutchings 1988)

= 0.05 x 2.3585 mg DM l^{-1} (= 1/0.424 = 2.3585mg DM. mgC^{-1}) (Table 2.2)

= 0.118 mg dry mass l^{-1}

= 0.118 x 10 = 1.18 mg wet mass l^{-1} (H. M. Verheye, pers. comm.)

Horse mackerel mass was calculated from the equation:

$$WBM = 0.0093685\ TL^{2.9601}$$ (M. Kerstan, MCM, unpub. data)

and gave average values of 41.1g and 6.3g wet mass for large and small juvenile horse mackerel, respectively. Daily ration values of 2, 3, 4, 5 and 6 % WBM were calculated for small and large juveniles and the time taken to attain these values calculated using the above data.

Fish mass: 41.1g large juvenile horse mackerel

Feeding $rate_{LL}$: 1.644g = 10.23 l $fish.^{-1}$ $min.^{-1}$ x 1.18 mg wet mass l^{-1}

= 12.0714 mg wet mass $fish.^{-1}$ $min.^{-1}$

Daily ration = 4% of 41.1g = 1.644g wet mass $fish.^{-1}$ d^{-1}

Time to consume daily ration for 41.1 g fish = $\frac{1644 \text{ mg wet mass fish.}^{-1} \text{ d}^{-1}}{12.0714 \text{ mg wet mass fish.}^{-1} \text{ min.}^{-1}}$

= 136.2 minutes per day

= 2.27 hours per day

These sample calculations suggest that the time required by large juvenile horse mackerel to obtain a daily ration of 4% WBM was 2.27 hr. when feeding on large zooplankton. Similarly for large juvenile horse mackerel feeding on small zooplankton the time was 1.83 hr. For small juvenile horse mackerel these values were 0.54 hr and 1.00hr for small and large zooplankton respectively (Fig. 5.3)

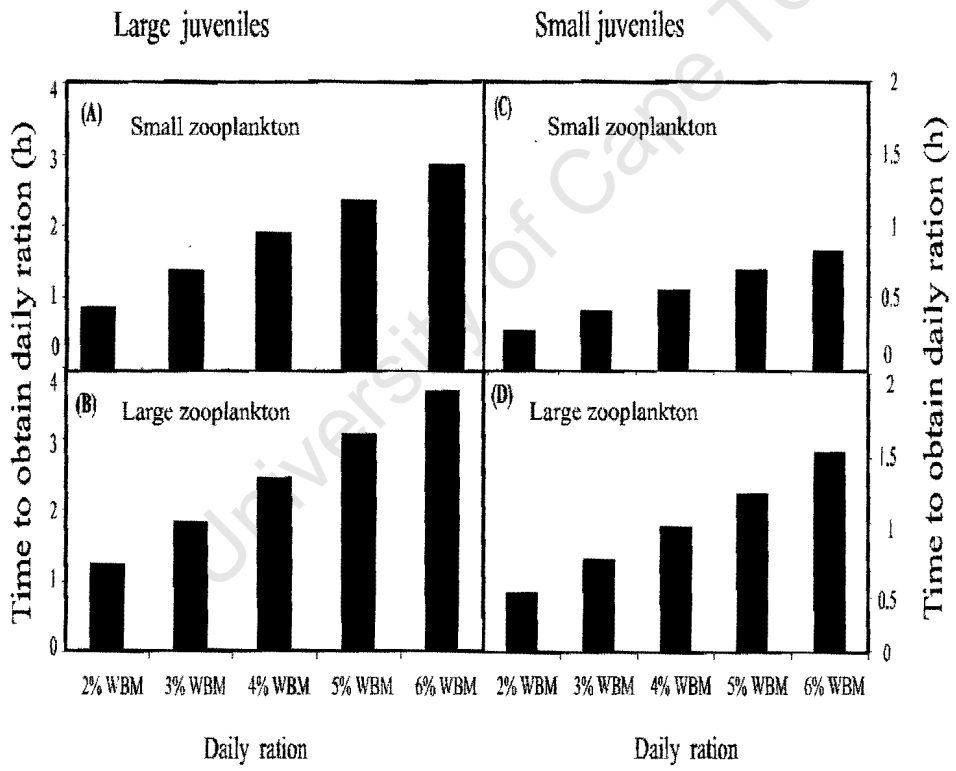

Fig. 5.3. Time to attain daily ration for large (a, b) and small (c, d) juvenile horse mackerel feeding on small (a, c) and large (b, d) zooplankton respectively.

Small juveniles appear to obtain their daily ration faster than large juveniles, and both fish sizes obtain their daily ration faster when feeding on small zooplankton than on large zooplankton. This difference might be due to very high concentrations of small zooplankton when compared to large zooplankton (a four -fold difference).

The time estimates for juvenile horse mackerel to attain the daily ration seem to be very similar to the findings reported by Pillar and Barange (1998) who reported that horse mackerel appeared to feed more frequently in the late afternoon, exploiting the near-bottom aggregation of prey during the day, before ascending into the midwater at night when feeding have ceased. Given also that horse mackerel had a rapid rate of gut evacuation, there were speculations that their migration to warm surface waters at night serve to stimulate and increase digestion rates so that consumption during the next feeding period is not limited by undigested food remaining in the stomach (Pillar and Barange 1998).

5.3: Comparing the feeding behaviours of horse mackerel, sardine and anchovy

In the southern Benguela ecosystem, anchovy undergo diel vertical migration, rising to the surface and dispersing at night, and aggregate and descend during the day (Thomas and Schülein 1988). The migrations and feeding patterns of these fish are associated with the diel vertical movements of their prey e.g. large calanoid copepods and euphasiids,

which ascend from the bottom to the surface layers in the evening (Hutchings 1985). For juveniles on the west coast, feeding peaks between dusk and midnight and between midnight and dawn for adults on the South Coast (James 1987). Anchovy are omnivores feeding both on phytoplankton and zooplankton with the latter being the more important in their diet than the former. Calanoid copepods and euphasiids are the major prey types in both West and South coast study areas (James 1987). Particulate (raptorial) feeding is a predominant mode of feeding used by anchovy, although they can also be filter feeders. Experimental data (James and Findlay 1989) has shown that juveniles and adults filter feed on small particles (< 0.5mm) and selectively feed raptorially on items greater than 7.0mm.

Sardines also undertake diel vertical migration but not to the same extent as anchovy, they tend to form small, scattered schools at night and dense schools during the day. They generally remain in the upper 20m of the water column (Hampton *et al* 1979, Thomas and Schülein 1988). The feeding periodicity of sardines is size dependent, with small (<25 g) fish feeding mainly around sunset, whereas large fish appear to feed continuously (van der Lingen 1999). Continuous feeding suggests a filter-feeding mode, and in smaller sardines the observed periodicity suggests that they are particulate feeders. Experimental studies have confirmed that sardines are able to capture phytoplankton through filter feeding (van der Lingen 1994) although the feeding behaviour of juvenile sardine has not been examined experimentally. Field investigations have found them to

be more zooplanktophagous than adults (Hand and Berner 1959, King and Macleod 1976), suggesting that juveniles employ particulate feeding to a greater degree than adults (van der Lingen 1999).

Horse mackerel undergo diel vertical migration in the southern Benguela ecosystem (Pillar and Barange 1998). They ascend as a population from the bottom into midwater around sunset, remain there throughout the night and return to the seabed around dawn. This movement appeared to be for reasons other than feeding; stomach fullness and prey freshness decreased markedly after sunset and there was no feeding during the night in all the diel studies done. This suggests that feeding only occurs during the day when horse mackerel are near the bottom and feeding on the aggregations of copepods and euphasiids (Pillar and Barange 1998). The present experimental studies confirm that juvenile horse mackerel are visual particulate feeders on zooplankton, explaining their day time feeding behaviour.

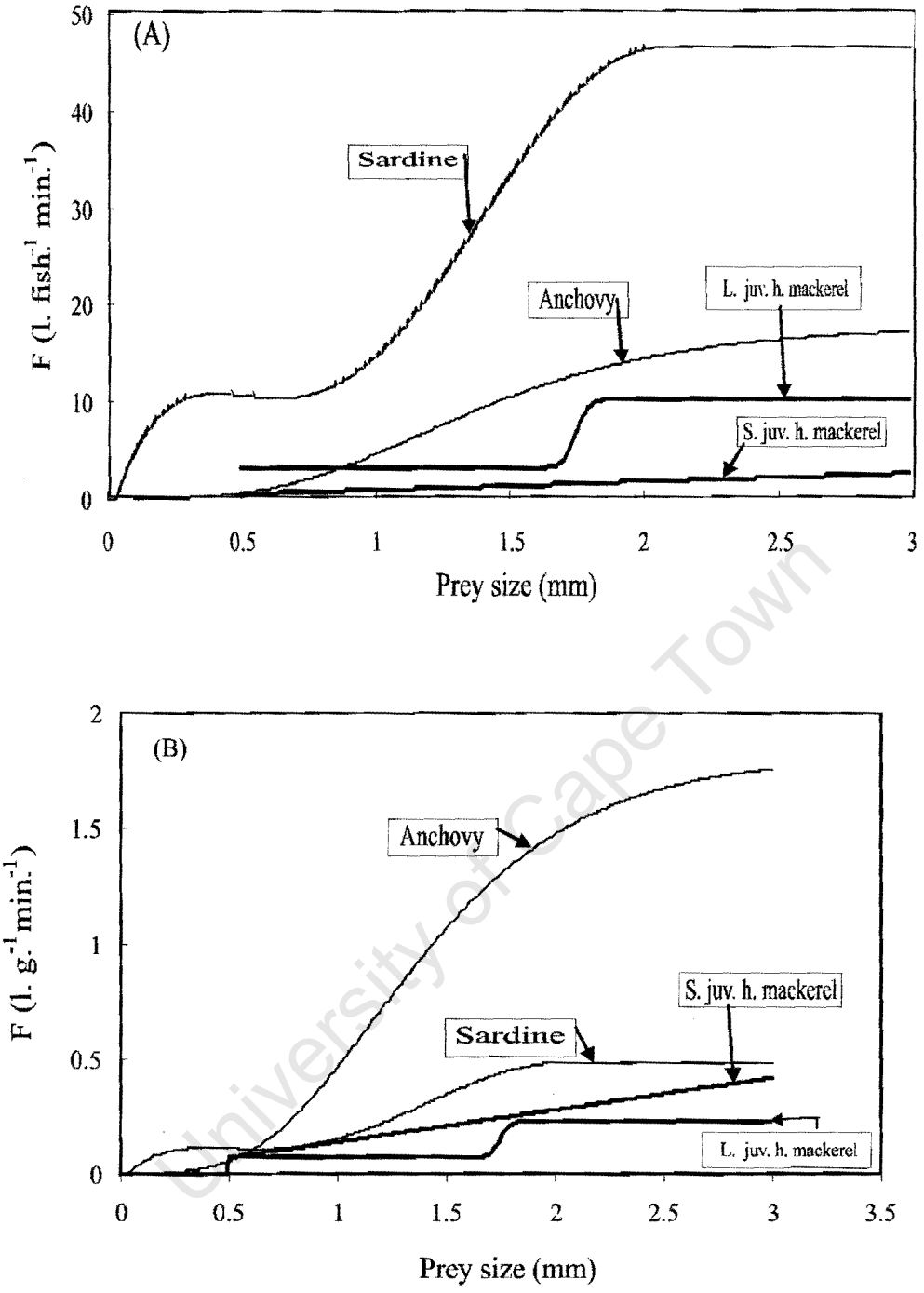

Fig. 5.4 Predicted clearance rates (F) as a function of prey size for horse mackerel (large and small), sardine and anchovy. (A) F expressed on a per fish basis and (B) on a per gram basis (weight standardised). Clearance rate equations were obtained from van der Lingen (1994) for sardine and James and Findlay (1989) for anchovy.

Predictive equations of clearance rate as a function of particle size can be used to facilitate comparisons of feeding behaviour between sardine, anchovy and horse mackerel off the southern African coast (Fig 5.4). When compared on a per fish basis sardine shows much faster clearance rates than anchovy and both large and small juvenile horse mackerel. When the clearance rates are standardised and expressed as a function of fish weight, anchovy are by far the most efficient species and clear large (>6.0 mm TL) prey more rapidly than the other species. Sardines are more efficient than the other species for small prey (< 0.6 mm TL). Juvenile horse mackerel show weight and standardised clearance rates that are similar for both large and small fish and are the lowest values of all

The information obtained from this study can be used to compare the feeding behaviour of juvenile horse mackerel with those of sardine and anchovy, other major zooplanktivores in the southern Benguela. Such a comparison should be valid, since similar experimental methodology was used to examine the feeding behaviour of the three species (see van der Lingen, 1994, for sardine, and James and Findlay, 1989, for anchovy).

The dominant feeding mode of sardines is filter-feeding, whereas anchovy are mainly particulate feeders and juvenile horse mackerel do not appear to filter feed at all. Both sardine and anchovy can switch between feeding modes but horse mackerel use only one

mode of feeding. All three species regulate their swimming speed in the presence of planktonic food, with sardines regulating the speed according to prey concentration and anchovy according to prey size, while horse mackerel regulate theirs according to both prey size and concentration in large juveniles, whereas small juveniles were not affected by either parameter.

Conclusions:

The results of this study have shown that horse mackerel are obligate particulate zooplanktivores, feeding mainly on large copepods and mysids, used as 'surrogate euphasiids'. They select their food on the basis of prey size, selecting the largest particles available. Swimming behaviour of juvenile horse mackerel differed according to the food particle abundance. When the food particles were plentiful the fish increased their swimming speeds which later decreased with decreasing prey abundance. Large and small juvenile horse mackerel responded differently to some factors. Large juveniles regulated their swimming speed according to prey size and prey concentration whereas small juveniles were not affected by these parameters.

When comparing horse mackerel with other zooplanktivores in the southern Benguela ecosystem, horse mackerel fall between the sardine and anchovy in terms of feeding behaviour although they are more similar to anchovy i.e. anchovy are omnivores but predominantly feed by particulate feeding, sardines are mainly filter feeders and horse

mackerel are obligate particulate feeders. These results can be of some importance because they allow for a better understanding of the trophic position of horse mackerel in the southern Benguela system, and can be used in mass-balance trophic models, giving a baseline for energetic studies.

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